ANALYTICAL PALEONTOLOGY: PATTERNS OF TAXONOMIC EXTINCTION

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## ABSTRACT

## ANALYTICAL PALEONTOLOGY: PATTERNS OF TAXONOMIC EXTINCTION

By

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A simulation model was designed to investigate the relationship between taxonomic duration and extinction probability. In this model, a group of mutually interacting species are monitored through space and time. The space is a fitness space in which there exists an optimum fitness position. Position of a species relative to the fitness optimum controls its reproductive success and thereby determines its potential for survival under the forces of selection. Change in the position of the fitness optimum alters the relative fitness of a particular species location, and a species occupying a low fitness position for an extended time undergoes extinction. Speciation occurs when area becomes available through extinction at the same time a probabilistic isolation event occurs.

Output from the model was expressed in life-table format, and taxonomic survivorship curves were drawn. Different boundary conditions, representing different biological constraints, were used so that factors producing systematic alteration in taxonomic survivorship data could be identified. Specific factors considered were: 1) availability of living area; 2) intensity of selection; 3) resource instability; and 4) methodological treatment of living and extinct taxa.

The principle conclusions of this analysis are: 1) A simple Darwinian-Mendelian evolutionary model can produce linear taxonomic survivorship curves under conditions of dynamic evolutionary change; stable non-dynamic conditions tend to produce concave or convex survivorship curves.

2) External time-related factors can modify taxonomic duration patterns; analysis of age-related patterns requires removal of temporal effects. 3) Inclusion of living taxa in the life-table compilation for extinct taxa can substantially alter the survivorship curves. 4) Inclusion of deterministic as well as stochastic components in the model, and removal of taxonomic restraints on lineage shape and size produced cladograms which are not the result of preconceived notions of phylogenesis.
5) Without taxonomic restraints, the general cladogram shape produced by the simulation appears reasonable when compared to clades for living and fossil organisms.

## ANALYTICAL PALEONTOLOGY: PATTERNS OF TAXONOMIC EXTINCTION

By

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#### INTRODUCTION

The spectrum of paleontological research encompasses both the systematic analysis of fossil organisms, and an attempt to extract from this systematic analysis, the fundamental principles of phylogenesis and evolution. Identification of meaningful macroevolutionary parameters requires careful analysis of data sources and their potential biases. Characterizations of macroevolution have been based on measurements of faunal diversity, both temporal and spatial(Raup, 1972; Schopf, 1974; Stehli, 1969; and Valentine, 1971, 1973b), and extinction rates(Boucot, 1975; Simpson, 1953; and Van Valen, 1973). The controversies which surround these areas of information have generated much recent literature(reviews by Valentine, 1973; Van Valen, 1973). Analysis of the fossil record has not produced unequivocal solutions to all of these problems.

As an alternative to direct analysis of data from the fossil record, it is possible to design computer simulation models to assist in the investigation of evolutionary processes. This approach can be uniquely effective in paleontology because evolutionary processes operate on a time scale which often makes experimental or analytical problem-solving techniques impractical. Complex genetic and evolutionary systems can be simulated in mathematical terms, conforming to the accepted models of

evolutionary processes and operating at a chosen level of complexity. Assumptions used to construct a simulation model determine the degree of correspondence between the model and the simulated system. Because boundary conditions are known, comparison of results produced by the model under different biological constraints provides an effective method for quantitative evaluation of complex systems.

Although the fossil record provides the only source for documentation of large-scale organic evolution, it has contributed little to our understanding of evolutionary mechanisms (Raup and Stanley, 1971). A recent trend toward a nomothetic paleontology(Raup and Gould, 1974) is based on the conviction that it is possible to extract evolutionary principles from the fossil record. Within this framework, the direct analysis of empirical fossil data is the first step, preceded of course, by sound taxonomic studies. The next step involves testing general evolutionary models by comparing predictions of the models with observations from the fossil record. This link is often difficult to make, and simplification by means of simulation techniques can be extremely helpful for establishing the connection between general evolutionary models and the empirical fossil record.

In this study, a group of mutually interacting species are monitored through space and time. Each species is symbolically represented by a variable number of genotypephenotype classes, and each class contains a variable number

of individuals. The space occupied by the species can be considered to be a fitness space in which there exists an optimum fitness position. The position of a species, relative to the fitness optimum controls its reproductive success, and thereby determines its potential for survival under the forces of selection. Species are considered to be in competition with each other, because change in the position of the fitness optimum alters the relative fitness of a species location in space. Species occupying a low fitness position for an extended time period are reduced below a critical number of individuals by selection, and undergo extinction. Probability of speciation is controlled by the density of species in fitness space and the genetic variability within the species. The inherent genetic variability is assumed to provide the raw material for evolutionary change(Bonner, 1974). This variability may or may not be reflected in phenotypic variability.

This model was designed to examine several specific paleontological problems, related to patterns and rates of taxonomic extinction. Extinction of taxa (and replacement) is responsible for temporal change in diversity. Of the various possible methods that characterize extinction rates and allow analysis of the factors influencing them, an effective approach is that of Van Valen(1973). His method involved the use of survivorship curves, plots showing the proportion of taxa surviving for various time durations. A logarithmic ordinate was used so that when the taxonomic extinction rate is constant,

a straight line results. After analysis of 25,000 taxa of plants and animals from the fossil record, Van Valen concluded that the survivorship curves were essentially linear, with varying slopes reflecting differences in extinction rates. A linear taxonomic survivorship curve indicates extinction probability is constant throughout the duration of the taxon under investigation. Several authors have recently commented on this question and suggested possible explanations for the linearity or departure from linearity of taxonomic survivorship curves for extinct taxa. Raup(1975) reviewed the problem and isolated biases inherent in data treatment. He also suggested linearity tests which could be used to make the data statistically reliable. Sepkoski(1975) presented stratigraphic biases, potentially affecting the shape of survivorship curves. He pointed out that because time intervals representing taxonomic durations are estimates, systematic biases could cause non-linear survivorship curves to appear linear. Incomplete sampling was also shown to contribute to this systematic error.

Data produced by the simulation model developed for this study was plotted as survivorship curves. Different boundary conditions, representing different assumed biological constraints, were considered so that factors responsible for changes in the survivorship curves could be identified. The specific factors under consideration as potential modifiers of extinction rates, and therefore responsible for irregularities in taxonomic

survivorship curves were: 1) availability of living area;
2) intensity of selection; 3) temporal changes in genetic
variability; 4) resource instability; and 5) a procedural factor
involving the effect of including data for living taxa in the
data pool for extinct taxa.

In this paper, previous studies utilizing simulation models for investigation of biological-paleontological problems are reviewed. The basic characteristics of the simulation model used in this study are discussed and specific output from the model is compared to data for living and extinct organisms. The degree of correspondence between output from the model and data from living and extinct organisms is dependent upon the range of boundary conditions imposed. When the boundary constraints are biologically reasonable, operation of the model produces results not unlike those produced by nature. This aspect of simulation modeling is very useful, allowing extreme conditions in nature to be studied. In this particular case, conditions of very high interspecific competition or resource instability as well as very low competition and constant resource conditions can be simulated.

The principal conclusions of this analysis are: 1) A simple Mendelian-Darwinian evolutionary model can produce linear taxonomic survivorship curves; 2) Taxonomic survivorship curves systematically depart from linearity as competition between taxa is reduced; and 3) Inclusion of living taxa in

the analysis of extinct groups alters the survivorship curves in a predictable manner. Resource instability has not, within the context of this model, produced significant alteration of extinction rates. In addition, the effects of temporal changes in genetic variability are not resolvable under the current mode of operation of the model. This is an artifact of model design, and will be a topic for additional investigation.

A model such as this one can provide insight into the operation of evolutionary processes and establish the reasonableness of alternative hypotheses. If an accepted evolutionary hypothesis is not supported by the model, the alternatives are: 1) The model does not adequately simulate the system; 2) Geologic time factors are affecting the results; 3) The original data was incorrectly collected or interpreted; or 4) The evolutionary hypothesis should be reevaluated.

#### **PREVIOUS STUDIES**

The fossil record has contributed little to our understanding of basic evolutionary mechanisms(Raup, 1971). It does, however, provide the only source for documentation of largescale organic evolution. Retrieval of information from the fossil record requires accurate taxonomic studies, transforming the raw data to a form which is useable in quantitative studies of diversity, and in analysis of evolution and extinction rates. Simulation of evolutionary patterns by computer provides an alternative approach to the direct analysis of empirical data from the fossil record.

Computer models can be used to simulate evolutionary mechanisms at the genotypic level or to investigate the operation of large-scale evolutionary processes. Fraser(1959) developed a model simulating the variability in a polygenic system in which the phenotype was controlled by several genes and different assortments of genes produced similar phenotypes. A situation then occurs where genetic variability is high, but phenotypic variability is low. Fraser concluded that selection could favor low phenotypic variability without modification of genetic variability. Another early study by Crosby(1963) involved genetic anomalies in the primrose population in England. Differences in the movement of pollinating insects in the area, influenced

by the spatial distribution of insect habitats, were thought to produce differences in interbreeding. By making assumptions about the behavior of pollinating insects, a simulation model was developed which produced genetic distributions very similar to those identified in the wild primrose population.

A comprehensive evolutionary model was developed by Papentin(1973). His main goal was to identify the specific model which would produce maximum rates of adaptation. A system containing three arrays was considered: genotype, phenotype, and environment; and four operators: selection, mutation, recombination, and alteration. Evolutionary processes were represented by actions of the operators on the arrays. Population fitness increased with the number of generations, and evolutionary rates increased with variance of fitness and selection pressure. Rates of evolution increased with the number of genotypes considered, but decreased with the number of loci. Free recombination was shown to be optimal, and for a given system, there was an optimal mutation rate. Epistatic gene effects tended to decrease evolutionary rates. Maximum rates of adaptation were obtained by large, haploid sexual populations under strong selection pressure, and exhibiting a low degree of epistatic gene interactions. Papentin concluded that the exact design of an evolutionary model must be a function of the type of problem under investigation, and the level of generality must also be chosen to fit the specific problem.

Raup and Gould(1974) and Raup, et. al.(1973) used computer models to investigate aspects of macroevolutionary processes. Their major concern has been with the causes of morphological order in evolutionary trees. They point out that much evolutionary interpretation has been based on an assumption of directional causes in macroevolution, a direct outgrowth of the observation of "order" in the fossil record. Using random decisions to determine whether a lineage undergoes diversification, extinction, or is allowed to persist unchanged, their simulation studies have shown that directional selection forces may not be required to produce morphologic trends, character correlations, convergence, and related changes. Totally stochastic systems were shown to replicate many of the evolutionary patterns observed in the fossil record.

Other quantitative studies have addressed the question of rates of extinction and speciation. Using publications such as The Fossil Record(1969) and the Treatise on Invertebrate Paleontology, Van Valen(1973) compiled life tables (taxonomic durations) for 25,000 taxa and indicated that his data support a constant extinction rate within a given subgroup of a homogeneous higher taxon. He pointed out in a reply to criticism by Hallam(1976) that he did not argue that extinction probability was independent of age, but that the mean probability of extinction was constant over a long period of time. Van Valen offered a possible explanation for constancy of extinction

rates in which he suggested that a successful adaptation by one species has a net negative effect on all other species, and causes the overall species environment to deteriorate at a stochastically constant rate. If the positive and negative effects are on the average, equal, then the average intensity of selection and rate of adaptive evolution would be constant through time. Both Sepkoski(1975) and Raup(1975) investigated aspects of this model via simulation studies. Sepkoski concluded that less than 25% of the survivorship curves presented by Van Valen support the conclusion of constant extinction rates. Raup questioned the survivorship analysis techniques, and proposed methodological changes and statistical tests for linearity. Some deviation from linearity, according to Raup, may be due to monographic effects (i.e. artifacts of the literature) related to the taxonomy of supraspecific taxa.

The Fraser model(1959) was an attempt to deal with selection at the phenotype level which does not necessarily produce modifications in the genotype. Papentin(1973) modeled genetic changes during adaptation and investigated factors controlling rates of adaptation. The Raup-Gould model(1974) operated at the morphological level, generating phylogenetic trees that were then compared to evolutionary trees for a variety of organisms, derived from the fossil record. The model developed for this study simulates the basic components of evolution: reproduction, natural selection, extinction,

and speciation. Patterns of diversification are displayed by generating cladograms for simulation data. Data is also extracted in the form of taxonomic durations and plotted as taxonomic survivorship curves. Characteristic survivorship trends are identified and related to specific boundary conditions. By analogy, similar factors affecting survivorship of fossil and living taxa can be recognized. This model is specifically designed to identify trends which could be produced by directed (non-random) aspects of evolutionary processes. These directed causes, together with the non-directed(random) processes isolated by Raup and Gould, should provide a more complete understanding of macro-evolutionary processes and products.

#### DEVELOPMENT OF THE EVOLUTIONARY MODEL

General Description of the Model

Darwinian evolution is a process which acts at the phenotypic level(Lewontin, 1974) and is capable of producing changes in the phenotype distribution of a population. The change in phenotype is not directly related to genotype change. Because of dominance effects, recombination, extranuclear inheritance, pleiotropy, and canalization, modification at the genotype level may be out-of-phase with phenotype change in response to selection. For investigation of patterns of diversification and morphologic change during macroevolution, the genetic system should be modeled at a level of complexity analogous to the information content of the fossil record. Simpson's work on evolutionary patterns (1953) is based on the assumption that large-scale phenotypic change observed in the fossil record is a true reflection of evolutionary change. This assumption is reasonable, based on the quality of resolution of the fossil record.

Choice of an approach for modeling evolutionary processes was based on several considerations. According to Crosby(1973), there are two methods for modeling genetic systems: 1) algebraicutilizing mathematical techniques from population genetics; and 2) creation of model organisms- inducing them to behave

in a way analogous to the behavior of real organisms. Arrays of these organisms represent the model population. The second alternative was chosen for this study because the complexity of theoretical genetics would be difficult to reduce to the level of generality appropriate for this study.

The simulation developed for this study is based on a simple Darwinian-Mendelian evolutionary model. The initial species population is generated and placed in three-dimensional fitness space. Each species occupies a fixed volume of fitness space, and coordinates of species positions can be specified. A position of maximum adaptive fitness is also specified. The Euclidean distance from a species to this maximum fitness position is used to determine the fitness of a species during a given generation, and ultimately to establish its survival potential as it competes for resources with other species. This general model of resource competition resembles the Red Queen Hypothesis, proposed by Van Valen(1971; 1973). He visualized species occupying an adaptive landscape in resource space. Total resources are fixed, and a depression in the landscape in one location necessitates a compensatory increase in elevation in another area. This suggests that a successful adaptive response by one species produces a net negative effect on all other species. Species occupying the landscape attempt to maximize their share of the resources, and the fitness of a species is proportional to the amount of resources it

controls. This resource control is the feature which is optimized by natural selection, according to the basic Red Queen Hypothesis.

Resource space-fitness space in the model is not a static feature but undergoes change each generation, not in total quantity of resources but in distribution of resources. Change in resource distribution was used to represent environmental variability, which causes the relative fitness of species to change. This dynamic feature of the resource space was designed to allow either minor or major shifts, so that concomitant effects on species populations can be monitored. A species which continues to successfully control its resources gains individuals; likewise, a species which loses control of resources decreases in total number of individuals. If the loss of fitness (resources) is severe enough, the species becomes extinct as the total number of individuals falls to zero.

The total number of species occupying resource space varies about an equilibrium value, determined within the simulation. The application of biological-ecological equilibrium models in paleontology is part of the nomothetic trend, lauded by Raup et. al.(1973). This strategy allows the complexity of events in the real world to be adequately simulated by models using relatively few generating factors, according to Raup et. al. The probability of speciation during

a given generation is determined by the overall density of species in fitness space, and the internal variability of the individual species. Mayr(1963) suggested that speciation occurs when internal genetic variability becomes available to a species at a time of increasing (or unexploited) resources. Several mechanisms for releasing this variability are proposed, but for purposes of this model, the species with high genetic variability in a generation where resources are available has the highest probability of speciation. When a new species is formed, it is given a fixed quantity of resources (a number of individuals + a position in fitness space), and then must compete to maintain or gain more resources during the ensuing generations.

Each species undergoes reproduction once per generation. New individuals are produced from the parent population by randomly choosing two parents and combining their characteristics into one offspring individual. This part of the model is designed so that four times as many offspring are produced as survive under conditions of average species fitness. This allows selection to reduce the population size each generation, based on the relative fitness of all species and the survival value for individuals within the species. Offspring replace the parents in the population, a method which accelerates the generation-to-generation change in the simulated population. This general reproduction model is similar to one suggested

by Fraser and Burnell(1970). It produces a change in the character and number of individuals in a species based on its competitive success in the previous generation. The total number of individuals in resource space is governed by an equilibrium value which controls the survival value of the fittest species. This survival value fluctuates so that it reaches a maximum when the total population size is increasing, and a minimum when the population size is decreasing.

A highly generalized flow chart for the computer model is shown in Figure 1, and a more detailed flow chart is included as Appendix A. The remainder of this section discusses each component of the simulation in detail, developing the conceptual and mathematical framework for the computer model.



Figure 1. General organization of simulation model.

Components of the Model

Establishing Species Centers

The original species are placed in a three-dimensional fitness space. Coordinates defining the species centers are determined by the use of random numbers, generated by an internal library function. These numbers are then adjusted so they fall between zero and the dimensions of the fitness space into which the species are placed. This adjustment does not destroy the randomness of initial species position because it is accomplished by making the same modification in all location coordinates. The procedure is as follows:

R1 = RANF(-1)
IR1 = R1 \* (DSPACE - 3) + 2
X(I) = IR1 \* XUNIT .....Y(I) & Z(I)
where RANF is an internal library function
which generates a random number
falling between 0 and 1
DSPACE is the dimension(X, Y, and Z directions)
of fitness space
XUNIT is the unit of distance in the
X direction (equal to YUNIT & ZUNIT)

A three-dimensional coordinate space was used to represent resource-fitness space, mainly for ease of data treatment and visualization. After the second species center is located, the Euclidean distance between each species pair is calculated and compared to a minimum distance. This comparison is necessary

to solve computational problems occurring if species centers fall too close to each other. If the centers are too close, the program returns and randomly chooses new X, Y, and Z coordinates for the species center.

Rather than locate all individuals constituting a species population in the same position in fitness space, each species center is surrounded by 26 genotype-phenotype locations which are termed classes. After the coordinates of a species center are calculated, the coordinates of the class positions are fixed as shown in Figure 2. Each class has a X-Y-Z coordinate as well as a "genotype" which specifies the position of the class relative to the species center and to the other classes. Table 1 displays the class numbering scheme with the class designations expressed in 3 x 3 x 3 coordinate space and the corresponding binary (diploid) genotype for the position of the class relative to an arbitrarily defined origin (Class 1 = 00 00 00). Each species can be considered a cluster of individuals in fixed positions relative to the species center, and occupying a region of fitness space.

Of the 27 class positions, seven are assigned individuals for the first iteration of the model. The seven classes initially occupied were chosen for reasons explained later in the paper. Eight additional classes are "open" and can be assigned offspring during reproduction. The remaining twelve classes are "closed" classes, simulating the "closed genetic system" as visualized



| CLASS | X-Y-Z<br>COORDINATES | BINARY WORD<br>(GENOTYPE) |
|-------|----------------------|---------------------------|
| 1     | 1 1 1                | 00 00 00                  |
| 2     | 1 1 2                | 00 00 10                  |
| 3     | 1 1 3                | 00 00 11                  |
| 4     | 121                  | 00 10 00                  |
| 5     | 122                  | 00 10 10                  |
| 6     | 1 3 3                | 00 10 11                  |
| 7     | 1 3 1                | 00 11 00                  |
| 8     | 1 3 2                | 00 11 10                  |
| 9     | 1 3 3                | 00 11 11                  |
| 10    | 2 1 1                | 10 00 00                  |
| 11    | 2 1 2                | 10 00 10                  |
| 12    | 2 1 3                | 10 00 11                  |
| 13    | 2 2 1                | 10 10 00                  |
| 14    | 222                  | 10 10 10                  |
| 15    | 2 2 3                | 10 10 11                  |
| 16    | 2 3 1                | 10 11 00                  |
| 17    | 2 3 2                | 10 11 10                  |
| 18    | 2 3 3                | 10 11 11                  |
| 19    | 3 1 1                | 11 00 00                  |
| 20    | 312                  | 11 00 10                  |
| 21    | 3 1 3                | 11 00 11                  |
| 22    | 321                  | 11 10 00                  |
| 23    | 322                  | 11 10 10                  |
| 24    | 323                  | 11 10 11                  |
| 25    | 3 3 1                | 11 11 00                  |
| 26    | 332                  | 11 11 10                  |
| 27    | 3 3 3                | 11 11 11                  |

# Table 1. Class numbering scheme and corresponding binary designations

by Carson(1975). These classes may become viable following major reorganization of the internal species makeup(Carson's flushcrash cycle), or when there are major changes in the environment. After species and class coordinates are calculated and stored, the original species population enters the main program and proceeds through the first reproductive generation.

#### Reproduction

This section is designed to simulate a form of sexual reproduction where the offspring replace the parents in the population. This could be considered sampling without replacement, because classes of the species available for reproduction in the following generation do not include the parents from the previous generation. The potential parent classes for the first generation are those initially assigned individuals. After one generation, additional parent classes become available whenever the offspring fall into the "open" classes.

Two parents are chosen at random from the occupied classes. Each class (1 - 27) has a genotype designation (Table 1). Genotypes of the parents are used to assign the offspring to one of the 27 classes as shown in the following example:

Parent 1 is randomly selected and belongs to class 7. The binary designation for class 7 is 00 11 00.

By analogy with simple Mendelian genetics, this parent can be considered a triple homozygote with each pair of digits corresponding to a gene locus. No further analysis is necessary for this parent because the haploid genotype is fixed; it must contain one allele from each loci, and therefore will have a designation of  $0 \ 1 \ 0$ .

Parent 2 is randomly selected and belongs to class 14. This is the completely heterozygous class with genotype 10 10 10. In this case, the allele provided by each locus is not fixed, but can be either 1 or 0. The resulting haploid genotype can be any one of the following combinations.

| 1 1 1 | 000           | 011 |
|-------|---------------|-----|
| στσ   | <u> 1 0 1</u> | 001 |
| ĪĪŌ   | <u>100</u>    |     |
|       |               |     |

Random numbers are again utilized for purposes of selecting the haploid genotype to be contributed by parent 2. For each of the allelic pairs, one of the two positions is chosen at random, and the three positions chosen are the genotype for the "gamete" provided by parent 2. If, for example,  $1 \ 0 \ 0$  were the genotype produced by parent 2, combination with the  $0 \ 1 \ 0$  genotype of parent 1 produces an off-spring with genotype

10 10 00

Referring to Table 1, this offspring can be assigned to class 13, which has an internal position of 2 2 1 in the species array (also refer to Figure 2).

The order of the alleles at each of the three positions in the genotype is not considered. Because of this factor, the probabilities of offspring falling into classes are unequal. As mentioned in the first section, not all classes are viable at any one time, nor are the viable classes necessarily occupied. The choice of viable and nonviable classes was based on the unequal probabilities. Table 2 demonstrates the reason for the higher probability of the "occupied" and "open" classes. As shown by Figure 2 and Table 2, the classes which were initially assigned individuals are the classes allowing the greatest

| CLASS | BINARY PERMUTATIONS | CLASS | BINARY PERMUTATIONS |
|-------|---------------------|-------|---------------------|
| 1     | 00 00 00            | 14    | 01 10 01            |
| •     | 00 00 01            |       | 10 01 01            |
| 2     |                     |       |                     |
|       | 00 00 10            |       |                     |
| 3     | 00 00 11            | 15    | 10 10 11            |
|       |                     |       |                     |
| 4     | 00 10 00            |       | 01 10 11            |
|       | 00 01 00            |       |                     |
|       |                     | 16    | 10 11 00            |
| 5     | 00 10 10            | 10    |                     |
|       | 00 01 01            |       |                     |
|       | 00 01 10            |       |                     |
|       | 00 10 01            | 17    | 10 11 10            |
|       |                     |       | 01 11 10            |
| 6     | 00 10 11            |       | 01 11 01            |
| •     | 00 01 11            |       | 10 11 01            |
|       |                     |       |                     |
| 7     | 00 11 00            | 18    | 10 11 11            |
|       |                     |       | 01 11 11            |
| 8     | 00 11 10            | _     |                     |
|       | 00 11 01            | 19    | 11 00 00            |
|       |                     |       |                     |
| 9     | 00 11 11            | 20    |                     |
|       |                     |       |                     |
| 10    | 10 00 00            |       |                     |
|       | 01 00 00            | 21    |                     |
|       |                     | 22    | 11 10 11            |
| 11    | 10 00 10            | 22    |                     |
|       | 01 00 01            |       |                     |
|       | 01 00 10            | ~~    |                     |
|       | 10 00 01            | 23    |                     |
|       |                     |       | 11 01 10            |
| 12    | 10 00 11            |       | 11 01 01            |
|       | 01 00 11            |       | 11 10 01            |
|       |                     | 24    | 11 10 11            |
| 13    | 10 10 00            | 24    |                     |
|       | 01 10 00            |       |                     |
|       | 10 01 00            | ~~    | 11 11 00            |
|       | 01 01 00            | 25    |                     |
|       |                     | 26    | 11 11 10            |
| 14    | 10 10 10            | 20    | 11 11 10            |
|       | 01 10 10            |       |                     |
|       | 10 01 10            | ~-    |                     |
|       | 10 10 01            | 27    | 11 11 11            |

Table 2. Allele permutations for classes 1 - 27

number of permutations in the alleles (5, 11, 13, 14, 15, 17, 23). They are also the classes in the center of each face of the three-dimensional cube, and class 14, the body-centered position. The open classes represent the next level of permutation (4, 6, 7, 10, 12, 16, 18, 22, 24), each having two allelic arrangements for a specific position. The closed classes are the remaining classes (1, 2, 3, 7, 8, 9, 20, 21, 25, 26, 27), and are located on the edges of the species block. Eight of these classes can be obtained by only one allelic combination, and thus are very low probability occurrences. Since order of the alleles within each pair is not considered, the number of different ways a genotype can be produced determines the probability of occurence of that offspring during reproduction.

## Genetic Variability of Species

Several aspects of genetic variability and its origin were considered when this section of the model was designed. Three distinct problems were addressed: 1) What is the relationship between phenotype and genotype? 2) How does the "closed" system of genetic variability(Carson, 1968; Mayr, 1963) participate in evolutionary change? and 3) How does environmental stability affect genetic variability(Ayala, et. al, 1975; Bretsky and Lorenz, 1969; Schopf, 1976)?

In the present mode of operation of the model, the phenotype and genotype were assumed to be directly related.

Modification in the genotype (except for order of allelesi.e.-  $\underline{1} \ \underline{0}$  and  $\underline{0} \ \underline{1}$  are the same genotype) produces a corresponding change in phenotype. This is not unreasonable because many authors (Anstey and Pachut, in press; Hawkins, 1964; and Raup and Michelson, 1965) have shown that large-scale morphological characters may be under the control of simple genetic systems. In addition, as suggested earlier in this section, the clarity of genetic data preserved in the fossil record limits the degree of complexity which a simulation model should contain.

Without the assumption of a direct link between genotype and phenotype, simulation models become more complex and the results are therefore, more difficult to interpret. Two distinct components must be added to a model for simulation of the more complex system: 1) a method for more than one genotype to produce the same phenotype; and 2) a method allowing one genotype to produce more than one phenotype. These specific components are not included in the present model. They can be incorporated for a second phase of operation which requires the foundation established by the basic model.

## Movement of Fitness Optimum

The fitness optimum is a position in X-Y-Z coordinate space which can be moved relative to the species locations. This section of the program was written to accomodate either

random or directional movement of the fitness optimum position. If movement is random, changes in the coordinates of the optimum position are determined by selection of new values from a Gaussian distribution (refer to Subroutine NORMAL in Appendix B). The old fitness optimum coordinates are used as means of the Gaussian distributions of possible values, assuring the most probable change in position is a small one. Larger coordinate changes are possible but have lower statistical probabilities. The standard deviation of the distribution is set independently for each coordinate direction and can be varied through time. Movement of the optimum fitness position is analogous to environmental instability, because each species becomes either more or less suited at his given location as a result of the change in position of optimum fitness. New distances are calculated each generation after the optimum has shifted, and relative survival rates are calculated. The following Fortran statement calculates the distance from the Ith species to the fitness optimum - (ENVX, ENVY, ENVZ):

DIST(I) = SQRT((X(I) - ENVX)\*\*2 + (Y(I) - ENVY)\*\*2 + 
$$(Z(I) - ENVZ**2))/DVAR$$

Distances were standardized by dividing the true Euclidean distance by DVAR, a number reflecting the internal species variability. This modification is based on the assumption that species with higher genetic variability should be given an advantage in their
struggle for control of fitness space(Mayr, 1963). This procedure was designed so that units used to measure distances in fitness space are not constant, but depend upon the species internal genetic makeup.

Directed movement of the fitness optimum can also be simulated. Coordinates of the fitness optimum position can be incremented by a chosen distance in fitness space. Following are the statements designed for this purpose:

> ENVX = ENVX + XSEL ENVY = ENVY + YSEL ENVZ = ENVZ + ZSEL

Where ENVX, ENVY, ENVZ are the X-Y-Z coordinates of the fitness optimum position

> XSEL, YSEL, ZSEL are the directed changes for the X-Y-Z, coordinate directions

By including options such as the one discussed above, the simulation model is made more general, and can be run with a greater variety of boundary conditions.

Selection

Selection is the primary cause of changes in gene frequencies(Mayr, 1963) and presumably one of the major factors in macroevolution. This section of the program was designed to accomodate either random or directed selection. The nature of the selection process is a function of the movement of the optimum fitness position. The movement is not necessarily equal in all three coordinate directions under deterministic change, and movement direction and magnitude are totally stochastic in the random movement option, as discussed above.

Coordinates of the species centers are ordered by a subroutine called SORT, which places them in a decreasing sequential list. This list, containing the species centers in order of increasing distance from the fitness optimum, is used to establish a fitness value for each species position. This is accomplished by assigning a maximum value to the species located nearest the fitness optimum position. The fitness space can be envisioned as a three-dimensional adaptive landscape in resource space. The species fitness is directly proportional to the amount of resource space it controls, and resource space is an adaptive factor which is a function of distance from the fitness optimum. The assumption is made that as a species becomes better adapted (occupies a position closer to the fitness optimum), it is able to control a greater amount of resource space.

Fitness of the species nearest the position of the optimum is arbitrarily set at the maximum allowable value. Each species position is then given a fitness determined by its distance relative to the position of the fittest species. Although Euclidean distances are calculated, the internal variability of the species is considered in the calculation so that a species with higher variability is given a competitive advantage in

terms of survival and reproduction in the next generation. The following set of statements demonstrate the procedure for determining the relative survival value of a species position:

FITSP = AVSUR + (CSPEC - 1) \* DSURV

where FITSP is survival value of species located nearest the fitness optimum

AVSUR is survival value for the mean species position

CSPEC is ½\*(NSPEC) where NSPEC = # species present

DSURV is the survival increment; this # controls intensity of species competition

Determination of AVSUR

AVSUR is used to maintain an equilibrium # of individuals

NHIGH = 1.25\*NTOTAL

NLOW = .75\*NTOTAL

SUMN = SUMN + NIND(I)

IF (SUMN.LT.NLOW) GO TO 1 IF (SUMN.GT.NHIGH) GO TO 2

1 AVSUR = AVSUR + .01 2 AVSUR = AVSUR - .01

where NHIGH and NLOW represent the upper and lower limits on # individuals

SUMN is the number of individuals

AVSUR is the survival value for the average species; it is used to determine the relative survival of all other species NTOTAL is the total number of individuals allowed; it is dependent on AREA, a variable reflecting fitness space available and species density

The survival value for each species position relative to FITSP is determined as follows:

SURV(I) = FITSP - (K\*DSURV)

where K is the position of a particular species relative to FITSP

DSURV is the survival increment

The number of individuals in a species is determined from the survival value. These individuals are not randomly distributed across the classes but are allocated according to the survival value of each class, determined in a way analogous to the procedure described above. Distances from each class within a species to the fitness optimum position are calculated. The classes are then placed in order of increasing distance by subroutine SORT. After selection has acted, the total number of individuals belonging in a species is known, but their class distribution must be calculated. The following procedure was used to determine the number in each class after selection:

 $X * a + (X-.01)b + (X-.02)c \dots = NIND(I)$ 

NIND(I) is known after selection and represents the number of individuals in the species Solving the above equation for X gives

$$X = \frac{\text{NIND}(I) + (.01b + .02c + .03d . . .)}{(a + b + c + d + . . .)}$$

The value of X can be used to determine the number in each class of species I. The .01 value is the class survival increment, analogous to DSURV at the species level. The number of individuals in the Jth class of species I is determined as follows:

$$SPECIES(I,J) = 4*OCCUP(J)*(X-POSIT(J)-1)*.01)$$

where SPECIES(I,J) refers to the Jth class of the Ith species

4\*OCCUP(J) refers to an assumption that four times as many individuals are produced as survive, giving the average species a .25 survival rate

POSIT is the position of the Jth class in the ordered sequence containing all occupied classes of species I

.01 is the increment used to determine class position

The selection section is designed so that survival values of individual species are dependent upon position relative to other species, and not absolute distance from the fitness optimum. This is based on the assumption that relative fitness and competition, rather than absolute fitness controls the probability of survival of a species. Within a species, classes in positions closest to the fitness optimum gain individuals at the expense of classes located further away.

## Extinction

Foin et. al. (1975) established three distinct evolutionary problems related to extinction: 1) How does the probability of extinction vary through time? 2) How does the probability of extinction change with taxonomic age? 3) How does the probability of extinction vary within one taxonomic group? In this study, the number of individuals in a species varies through time as the fitness of the species changes due to movement of the optimum fitness position. There is no specific set of operations for simulation of extinction. As an alternative to modeling extinction as a probabilistic event, the model was designed so that extinction occurs when the number of individuals in a species falls below a critical number. The total number of species present is then reduced, and the species density correspondingly decreases. Because this increases the probability of speciation, a balance exists between speciation and extinction. A very low probability event could move the fitness optimum a considerable distance, causing species located near the old position to lose many individuals in the ensuing generations. This might appear as a "mass extinction" in the output. The probability distributions for all three types of extinction can be calculated for the species in the simulation. Type (2)

is the extinction probability which Van Valen(1973) has dealt with. The statements controlling extinction are as follow: IF(NIND(I).LE.MINNO)GO TO 100 100 NIND(I) = 0 where NIND is the variable containing the number of individuals in species I MINNO sets the minimum # of individuals necessary for species persistence statement 100 assigns "0" individuals to species I

Speciation

Populations are given the opportunity to speciate during each generation. Speciation probability is a function of species density in fitness space and the internal variability of the species, arranged in a two-step hierarchial probabilistic sequence. The following set of statements summarize the speciation procedure:



NICSAT is a variable which changes as extinction removes species and speciation adds species. It represents a density function which depends on an operator selected value for AREA, the variable specifying the saturation number of species, and the value of NSPECP, the number of species currently inhabiting fitness space. R3 and R4 are random numbers, generated by the internal library function RANF. R3 is compared to NICSAT, and as shown in the statements above, a negative value for this comparison signifies the first step in speciation has been completed. This step can be considered analgous to the opening of an ecological niche through extinction, migration, or environmental change. Calculation of the PISOL(probability of isolation) value is analogous to asking the question whether the genetic variability necessary for reproductive isolation to develop is available. Mayr(1963) suggested that most of the divergence necessary for reproductive isolation occurs as the result of the utilization of genetic variants already present as polymorphs in the population. Speciation is not dependent upon the appearance of novel new mutations, but rather on exposure of inherent genetic variability, according to Mayr's thesis. For this reason, the PISOL value was determined by taking the ratio of internal variability of Species I (AVEVAR) to the maximum genetic variability found in any species in the population (MAXVAR). Then the PISOL value is compared to a second random number (R4), and a negative result in this probabilistic event produces successful

isolation. These two events, occurring in concert are sufficient to produce speciation. The new species center is assigned coordinates in fitness space within a fixed distance of the parent species. New species are given a number of individuals equal to 40% of the number in the parent species. Class coordinates are assigned and the species is available to undergo reproduction and selection in the next iteration of the model.

## APPLICATION AND DISCUSSION

When simulation models are developed, certain aspects of the system under investigation must be deemphasized while other aspects are considered. Loss of information in this manner is a "cost" of model building(Levins, 1966). Levins suggests there are three general types of costs: 1) degree of generality; 2) degree of realism; and 3) degree of precision. These factors should be considered in the model design, with acceptable operating levels chosen for the specific problem.

The general procedure followed when using a simulation model is to run the computer program with a range of known values or known distributions for the parameters under operator control. Boundary conditions can then be established for which the model produces results not unlike the real world. After these boundary conditions are identified, analogous factors responsible for natural variation can be extracted and analyzed. Because many systems do not permit experimental analysis for reasons of slow rates of change, system complexity, or unknown boundary conditions, the simulation approach may be the only procedure for obtaining information on the nature of the system.

The "costs" of model building should be explicitly defined during development of the model. The following discussion

analyzes some of the costs required for construction of the model used in this study.

I. Degree of Generality:

It is particularly important to choose the appropriate level of generality when designing a model. This requires careful analysis of the purpose of the model, prior to model development. A primary concern must be that the system is not misrepresented due to loss of information. At the same time, if the design is too complex, the advantages of simulation are lost because the model will be as difficult to understand as the natural system.

The complexity of a model of evolutionary processes can vary from duplication of molecular evolution at the chromosome level(Papentin, 1973) to studies of evolutionary patterns in the fossil record(Raup et. al., 1973). The level of generality of the model does not determine its validity or accuracy. The validity is directly related to the validity of the underlying assumptions. The accuracy is a measure of the model's ability to replicate the "real world" at the chosen level of generality.

This model was designed to monitor evolution at the population level. Although the model could be used for asexually reproducing organisms, the current mode of operation is based on sexual reproduction. The reproduction section describes the nature of this part of the model. The offspring genotypes are

a function of the parent genotypes, chosen randomly from occupied genotype classes, and a second random decision when alleles are chosen from heterozygous loci. This is a reasonable model for sexual reproduction, but does not incorporate chromosomal mutations, nor spontaneous allelic mutations. Since the purpose of the model was not specifically aimed at monitoring change in genetic composition at the chromosome level, these omissions are considered acceptable "costs" of the modeling process. An unknown "cost" must also be included: the validity of the underlying Darwinian Evolutionary process.

As previously outlined, the conceptual model for selection involves species competition for control of resources. The species are located in a three-dimensional space which also contains a position, specified as the fitness optimum. Species located nearest the optimum position are given a reproductive advantage, relative to more distant species. This reproductive advantage is realized in the total number of offspring produced, and in the specific classes occupied by those offspring. Within each species, the individual classes vary in fitness, and selection assures the classes in the best fitness position are favored during reproduction.

When an offspring falls into a class which is nonviable, it is rejected and new parents are chosen. In a natural system, selection is generally not this harsh, except in the case of lethal variants. The analogy between control of resource space

and position of the species relative to the fitness optimum position reflects a model design which, although generalized, includes the principal components of Darwinian natural selection.

Speciation and extinction are two other components of the model which require attention. Speciation may occur in response to several different conditions in the natural system. Allopatric speciation is thought to occur when peripheral populations are geographically isolated and undergo adaptive change in an environment different from the parent species(Eldredge and Gould, 1972). With phyletic speciation, the population undergoes a change in gene frequencies due to unidirectional change in the environment. A third type of speciation may occur when a population passes through severe changes in size due to varying selection intensities. According to Carson(1975), this speciation mode explains the formation of new species which are not adaptively different from the parent species.

It is probable that all three models describe a speciation mode that occurs in nature, either independently or in combination with the others. In this model, the probability of speciation for a species is determined at the end of each generation. This probability takes into account the number of extinctions occurring (an index of resource availability), a probabilistic isolation event based on a random decision, and the inherent genetic variability. A species with high genetic variability in a generation (iteration) where unutilized or unexploited resources

are available has the highest probability of undergoing speciation. Because the "geographic" position of the species determines both its variability (developed over a number of generations), and the portion of fitness space controlled by the species (resources), this corresponds most closely to the allopatric speciation model. However, it could be argued that at this level of generality, phyletic speciation is also a reasonable model.

No special consideration was given to changes in genetic variability during the speciation event. If Mayr(1963) is correct in believing that major genetic reorganization occurs during speciation, this model does not correctly simulate the speciation event.

Extinction takes place when the number of individuals in a species falls below a preset minimum number. This occurs when a species loses control of its resources by remaining in an unfavored position in fitness space for a number of generations. Extinction is modeled as another part of the evolutionary process of a species population, rather than an event requiring exotic explanations and mechanisms.

## II. Degree of Realism

It is difficult to evaluate this model on a scale of absolute realism because the natural processes simulated by the various sections are complex and in some cases, not well understood. The simulation was designed to consider conflicting

models or interpretations where possible. The "degree of realism" is a measure of how well the model utilizes the current understanding of natural evolutionary processes, because only if the model produces results, comparable to the "real world" can its value be determined. Although the degree of realism of a model is not directly related to the level of generality, it often becomes more difficult to be realistic in all aspects as the model is made more general.

The reproduction section is the most realistic for its level of generality. It effectively produces a population of offspring, genetically distinct from the parent population. However, because it relies totally on recombination for inducing genetic change in the population, it is unrealistic in its omission of spontaneous gene mutations as the ultimate source of new genetic material.

The allopatric model of speciation was followed because it is the most widely accepted in the literature. Allopatric speciation, according to Eldridge and Gould(1972), occurs in isolated peripheral populations where selection pressures are more intense or different from those pressures acting on the main body of the species. In these "fringe" conditions, phenotypes which are less successful in the central range of the species may thrive and become highly successful. Eventually they may become competitively equal or better fit than the parent population and replace them. This type of speciation does not

require the occurrence of a new and favorable mutant at a time when selection allows the new gene to become established in the population. Rather, as suggested by Mayr(1963), it relies on the genetic variability inherent in the population, and perhaps brought to expression by differences in the regulatory processes that control morphogenesis.

III. Degree of Precision

A simulation model can be designed to operate with high precision but precision does not imply accuracy. Accuracy can only be evaluated by determining the reasonableness of predictions based on the model, or by comparison of data generated by the model to similar results produced by natural systems. If the simulation does not produce reasonable results, several explanations are possible: 1) the system was incorrectly modeled; 2) boundary conditions were inaccurate; 3) original information was incorrect.

### OPERATION OF THE MODEL

In the evolutionary model designed for this study, certain parameters are assigned values at the beginning of the program; some vary about fixed or variable mean values; and others are assigned values within the body of the program, contingent upon a specific event or series of events. The following section discusses the parameters which are directly or indirectly under operator control, and therefore the parameters which are used to establish realistic boundary conditions for operation of the model.

#### Operator Controlled Parameters

# 1) Intensity of Species Competition

A parameter called DSURV allows the increment of survival to be set by the operator. With small survival increments, the difference in species survival as a function of position is reduced. This represents a situation where species competition for resources is low (abundant resource supply - low population density) giving all species approximately the same survival potential.

## 2) Variability of Fitness Optimum Position

The fitness optimum position can be controlled directly or indirectly by the operator. Direct control is possible through

the parameter DIRECT. This parameter can be used to produce unidirectional change in the coordinates of the fitness position, simulating long-term changes in environmental conditions or resource availability.

Indirect control is provided by the NORMAL subroutine, attached to the main computer program. By choosing to use this option rather than the DIRECT procedure described above, the fitness position is allowed to vary in a random fashion about the coordinates of the optimum fitness location in the previous generation. Different standard deviation values for the Gaussian distribution can be specified, causing the degree of fluctuation in the fitness position to vary. Because the actual coordinates are chosen from the Gaussian distribution about the previous mean, the most probable change in position of the fitness optimum is a small one, with large changes occurring less frequently. 3) Area Available for Occupation

The variable, DAREA is used to choose one of three possible area effects: a) area constant; b) area increasing; and c) area decreasing. The increment of area increase or decrease can be specified allowing simulation of loss or influx of resources. With increasing area, the total space available for occupation increases. This allows an increase in the equilibrium number of species by decreasing the DSURV value, the number determining the intensity of competition. When DSURV decreases, more species are able to successfully remain above the extinction level,

bringing about a higher species density and a lower probability of speciation. When the available area is occupied, the DSURV value increases. This increases competition between species and tends to drive more of them to extinction.

4) Number of Generations

The number of iterations is under operator control and is limited by financial restrictions rather than specific biological constraints. If the program was not run long enough for trends or variations about trends to become apparent, the number of generations could have a strong effect on the results. Sepkoski (1975) addressed a similar problem with regard to the information content of the fossil record. He concluded that systematic biases are produced when stratigraphic resolution is not good enough to reveal anomalous patterns of taxonomic duration. Simulation studies suggested that taxonomic durations must be long relative to the stratigraphic interval used to measure durations if non-linear survivorship curves are to be recognized. Similar problems must be considered when computer models are used to simulate long periods of time. It must be recognized that exact origin and extinction times are known in the simulation, whereas for fossil taxa of short duration, loss of information may produce systematic changes in the observed survivorship.

Additional Parameters Initially set by Operator

The remainder of the variables to be discussed are less important in their overall effect on the operation of the model. For this reason they are presented in list format with a brief statement. The complete computer listing can be found in Appendix II.

### LIST OF VARIABLES

- AVSUR AVSUR sets the initial mean survival at a specified number which later varies with the number of species present.
- CLDIST This is the value used to keep a minimum separation between species centers.
- DSPACE DSPACE establishes the dimensions of fitness space.
- ICLAS(I,J,K) This subscripted variable identifies the position of each of the 27 classes in the 3 x 3 matrix occupied by members of a species.
- IRANF This value defines the starting point for the random number generator in the random number table.
- IX, JX, IY, JY, IZ, JZ These values contain the genotypes for each of the 27 classes (either 1 or 0 in each position).
- MINNO The value provided for this number sets the minimum number of individuals allowed for species persistence.
- NAREA and DAREA These variables are used to call for constant or changing AREA, and to establish the increment of area increase or decrease.
- NINDPS This value sets the number of individuals per species for the initial reproduction run.
- NSPEC This value sets the initial number of species.

- SPECIE(I,J) This subscripted variable contains the class
   designations for the J classes of species I con sisting of occupied classes, open classes, and lethal
   (closed) classes.
- VX1 and VX2 These values are used to vary the effect that genetic variability has on probability of speciation.
- XUNIT, YUNIT, and ZUNIT The values for these parameters specify the units in the X, Y, & Z coordinate directions.

For identification of other variables calculated within the program, refer to the documented program listing in Appendix B.

#### METHODS OF SURVIVORSHIP

#### ANALYSIS

A complete picture of the mortality of a population can be obtained by construction of a life table. Several types of life tables have been used for a systematic approach to survivorship analysis(Odum, 1971). In general laboratory usage, the number of individuals surviving at specific time intervals (day, month, year) are monitored for a generation. A life table is then prepared consisting of several columns:  $1_x$  - the number of individuals surviving after a specific time interval;  $d_x$  the number of individuals dying during successive time intervals;  $q_x$  - death or mortality rate during successive intervals; and  $e_x$  - the life expectancy at the end of each interval. Curves plotted from life-table data can be used to determine the statistical properties of a population.

Survivorship curves have also been applied to the study of fossil lineages (Van Valen, 1973). When survivorship curves are used for analysis of taxonomic durations and extinction rates, stratigraphic ranges constitute the raw data. If the data is for extinct taxa, the information required is the time interval between origination and extinction. In living taxa, the time span between origin of the taxon and the Recent is used. Time-dependent biases in range data must be considered, as outlined

by Raup(1975). He also pointed out that systematic changes in the total number of coexisting taxa lowers the reliability of the survivorship trends. An equilibrium number of taxa is maintained in the model so that only minor random fluctuations occur. For paleontological data, assuming the world ecosystem has been saturated since middle Paleozoic(Raup, 1972), this source of error is not likely to substantially bias the large-scale trends observed in survivorship for fossil taxa.

To construct a survivorship curve, data from column  $l_x$ (number of survivors) is plotted on the vertical coordinate axis and duration of the taxa is plotted on the horizontal coordinate axis. The  $l_x$  value can be converted to a logarithm as suggested by Van Valen(1973), so that a straight line on the survivorship plot indicates a constant extinction rate for the group under consideration.

Three general types of survivorship curves are possible (Figure 3): I. Highly convex - characteristic of a group in which extinction rate was low until near the end of its stratigraphic range; II. Highly concave - resulting from a survival pattern where extinctions were prominent in an early or immature stage of the group; and III. Intermediate patterns, representing conditions where age-specific survival is nearly constant. If age-specific extinction rates are constant throughout the history of the group, the result will be a straight line on the semi-logarithmic plot. A stair-step or sigmoidal



Figure 3. Three general types of survivorship curves: I. Convex II. Concave III. Linear

survivorship curve indicates the extinction rate differs at successive stages in the phylogenetic history of the group.

All of the factors affecting speciation and extinction combine to produce the phylogeny of a taxonomic group. When survivorship analysis is applied to fossil populations, the fossil record must be interpreted as a record of normal mortality (raw data will be placed in the  $d_x$  column in the life table), or a census-type record representing mass mortality of a stable population (raw data will be placed in  $l_x$  column). The stratigraphic ranges for extinct taxa are  $d_x$  values, as are the durations of extinct taxa in this study. To obtain the  $l_x$ values, the  $d_x$  values must be cumulated as shown in the example in Table 3.

Figure 4 is the survivorship curve for the data in Table 3. To calculate the rate of extinction for an approximately linear curve, the formula for determining the decay constant of an exponential decay series can be used. It is expressed in survivorship terms (see Raup, 1975) as follows:

 $S_t = S_0 e^{-\lambda t}$ 

where  $S_0$  = the number of survivors at beginning of time period  $S_t$  = number of survivors after t time units  $\lambda$  = rate of extinctions per unit time

Table 3. Life-table for survivorship data plotted on Figure 4

| DURATION | d <sub>x</sub> | 1 <sub>x</sub> |
|----------|----------------|----------------|
|          |                |                |
| 1        | 30             | 179            |
| 2        | 19             | 149            |
| 3        | 14             | 130            |
| 4        | 14             | 116            |
| 5        | 19             | 102            |
| 6        | 12             | 83             |
| 7        | 17             | 71             |
| 8        | 9              | 54             |
| 9        | 6              | 45             |
| 10       | 9              | 39             |
| 11       | 5              | 30             |
| 12       | 3              | 25             |
| 13       | 5              | 22             |
| 14       | 2              | 17             |
| 15       | 1              | 15             |
| 16       | 6              | 14             |
| 19       | 3              | 8              |
| 20       | 2              | 5              |
| 21       | 1              | 3              |
| 23       | 1              | 2              |
| 32       | 1              | 1              |



Figure 4. General survivorship curve for data in Table 3.

The extinction rate can also be computed from the survivorship curve as follows:

$$\lambda = \frac{\ln S_0 - \ln S_t}{t}$$
or
$$\lambda = \frac{\log_{10} S_0 - \log_{10} S_t}{t \log_{10} e}$$

For the example above, assuming approximate linearity:

$$\frac{\lambda = \frac{\ln 179 - \ln 0}{40} = .130}{40}$$

Tests for Linearity

.

Van Valen(1973) did not use statistical procedures to test the linearity of his survivorship curves. He pointed out that because of the nature of the data, statistical significance or non-significance of the curves was not the important factor. He admitted that real sources of irregularity exist including sampling errors, but claimed that sample size and magnitude of the irregularities determined the significance of departures from linearity. In several examples, departure from linearity was shown to be the result of insufficient time since origin of the group.

Raup(1975), while critically reviewing Van Valen's work, agreed that uncertainties in the data and small sample size rendered statistical testing of debatable value but also pointed out that visual inspection of survivorship curves was not acceptable when important evolutionary questions were being considered. Because survivorship curves are cumulative frequency plots, points determining the nature of the distribution are not independent of each other. Unless a cumulative curve is highly concave or convex, it will tend to appear linear, and a statistical test sensitive to subtle departures from linearity would be very useful.

One of the most effective methods for statistical testing of exponential curves is the Total Lives Method of Epstein(1960a, b). This method makes use of the basic properties of Poisson processes, and was originally designed for use in determining changes in probability of failure of industrial equipment with age. If metal fatigue causes increasing probability of failure with age, a convex survivorship curve results. If fatigue does not produce an increasing likelihood of failure, the survivorship curves will appear linear.

The null hypothesis in the Total Lives Test is that the underlying distribution is exponential with constant mean life. Too many early failures (extinctions); too few failures in the early part of the distribution; or a change in failure rate during the test can be detected. The vocabulary and general procedure for performing the test is given in Raup(1975) and can be summarized as follows:

```
"total life" = sum of durations of all taxa in the
                       group before the taxon under con-
                       sideration became extinct
       Consider 100 taxa - 5 of the taxa lived 20 gener-
       ations, and 5 more became extinct after 30 gener-
       ations. Total Life calculation at the first
       extinction would be -
             (100 \text{ taxa}) \times 20 \text{ generations} = 2000
       For the second extinction event -
             2000 + (95 \tan x \ 10 \ generations) =
                                   2950 ....etc.
In general: If there are r taxa in all, with
             durations d_1, d_2 .... d_r, total
             lives are calculated by
             T_1 = r d_1
             T_2 = d_1 + (r - 1)d_2
             T_r = d_1 + d_2 + \dots + d_r
```

The sum of the first (r = 1) total lives is normally distributed if the survivorship is linear(Epstein, 1960 b). The mean of the normal distribution is given by  $(r - 1)T_r / 2$  and standard deviation by  $((r - 1)/ 12)^{\frac{1}{2}} \times T_r$ . The test for linearity of survivorship is performed by comparing the theoretical range of values in the mean total life acceptable at a chosen level of significance to the calculated sum of the total lives. If

 $\lesssim$  T<sub>i</sub> falls within the allowable range, the hypothesis of linear survivorship is accepted. Table 4 shows an example of this calculation, using the data from the example in the previous

|  |    | l                            | TOTAL LIVES | SUM OF  |
|--|----|------------------------------|-------------|---------|
|  |    |                              |             |         |
| $V(T_1 - T_{30})$                        | 1  | 179 + 1(0)                   | 179         | 30(179) |
| $V(T_{20} - T_{40})$                     | 2  | 179 + 149(1)                 | 328         | 19(328) |
| $V(\tau_{50} - \tau_{63})$               | 3  | 328 + 130(1)                 | 458         | 14(458) |
| $V(T_{64} - T_{77})$                     | 4  | 458 + 116(1)                 | 574         | 14(574) |
| $V(T_{70} - T_{06})$                     | 5  | 774 + 102(1)                 | 676         | 19(676) |
| V(Top - Tion)                            | 6  | 676 + 83(1)                  | 759         | 12(759) |
| V(1 + - 1 + 1 +                          | 7  | 759 + 71(1)                  | 830         | 17(830) |
| $V(\tau_{100} - \tau_{120})$             | 8  | 830 + 54(1)                  | 884         | 9(884)  |
| $V(\tau^{126} - \tau^{134})$             | 9  | 884 + 45(1)                  | 929         | 6(929)  |
| $v_{(\tau}^{135} - 140)$                 | 10 | 929 + 39(1)                  | 968         | 9(968)  |
| $V(\tau_{141}^{141} - \tau_{149}^{149})$ | 11 | 968 + 30(1)                  | 998         | 5(998)  |
| $V(\tau^{150} - \tau^{154})$             | 12 | 998 + 25(1)                  | 1023        | 3(1023) |
| $v_{(\pi}^{(155)} = 157)$                | 13 | 1023 + 22(1)                 | 1045        | 5(1045) |
| v ( 158 162)                             | 14 | 1045 + 17(1)                 | 1062        | 2(1062) |
| v(~163) <sup>-164</sup>                  | 15 | 1043 + 17(1)<br>1062 + 15(1) | 1077        | 1(1077) |
| v (~ 165                                 | 16 | 1002 + 10(1)<br>1077 + 14(1) | 1001        | 6(1001) |
| v (~166 171)                             | 10 | 1077 + 14(1)<br>1001 + 8(3)  | 1115        | 3(1115) |
| V(1172 174)                              | 20 | 1091 + 0(3)<br>1115 + 5(1)   | 1113        | 3(113)  |
| V(T175, -T176)                           | 20 | 1113 + 5(1)                  | 1120        | 2(1120) |
| $V(\tau_{177})$                          | 21 | 1120 + 3(1)                  | 1125        | 1(1123) |
| $V(\tau_{178})$                          | 23 | 1123 + 2(2)                  | 1127        | 1(1127) |
| $V(\tau_{179}^{-10})$                    | 32 | 1127 + 1(9)                  | 1136        | 1(1136) |

Table 4. Sample calculation of total lives test

 $\Sigma = 116358$ 

Under assumption of exponentiality, the 178 total lives  $V\tau_i$ , i = 1, 2 ..... 178 should be uniformly distributed in (0,  $V(\tau_{178})$ .

Theoretical mean for  $\sum_{i=1}^{178} V(\tau_i) = 178/2 (V\tau_i) = 178/2(1136) = 101104$ Standard Deviation =  $178/2(V\tau_i) = 3.85 + 1136 = 4374$ 

The 95% acceptance interval for hypothesis of underlying exponential distribution is given by:

 $101104 \pm 1.96(4374) = 101104 \pm 8575$ 

Acceptance interval = 92529 to 109679

Observed sum is 116358; This number is outside the acceptance interval. Therefore, null hypothesis must be rejected at the .05  $\leftarrow$  level.

section.

Because of the nature of the Total Lives Test, a variety of curves can fall within the 95% confidence limit. Calculation of the sum of durations allows a large deviation in one time unit to be cancelled by a small contribution from another time frame, so that the sum of total lives is not affected. Epstein also included tests for determining the type of deviation responsible for a nonlinear result. There is a test for abnormally early failure; a test for long first failure; a test for mean life fluctuation; and a test for abnormally long periods with no failure. These tests will prove useful in analysis of specific fossil lineages which show systematic deviation from linearity. Similiarly, taxonomic patterns produced by the simulation model can effectively be analyzed using these procedures.

## ANALYSIS OF SIMULATION RESULTS

The following sections summarize the principal categories of output produced by the simulation model. A detailed listing of the computer program is included in Appendix B. Units on parameters in different runs of the program are arbitrary, and actual values for the parameters are significant only when compared to values for other runs. Starting points for the random number generator were varied in repeated runs under the same boundary conditions so that effects of this change could be monitored. For all of the data used to illustrate systematic results of parameter changes, a minimum of five (5) separate runs were made to verify the results were repeatable. Precision remained high in the duplicate runs, except as noted, and no problems were apparent from this source.

## Effect of Competition Intensity

Operator induced changes in intensity of competition produce systematic changes in the survivorship curves. Three survivorship curves produced by runs with DSURV equal to .001 for I, .005 for II, and .008 for III are shown in Figure 5. All other parameters were held constant for these runs. DSURV is the variable which designates the survival value for an



Figure 5. Survivorship curves for varying levels of competition - selection.
increment of fitness space. When DSURV is set at .001, the difference in survival potential for two consecutive species positions is small, compared to a DSURV value of .008. A larger value for DSURV produces a situation where species position, relative to the fitness optimum is more important, analogous to conditions of increased competition. Because position relative to the fitness optimum ultimately controls the fate of a group, the DSURV variable is one of the most important parameters in the program.

Change in the shape of the survivorship curve from convex(I) to curves II and III, with increased slopes and more nearly constant age-specific extinction rates results from several factors. In curve I (DSURV = .001), intensity of competition was low and individuals surviving five generations had a high probability of surviving 20 generations. Extinction and speciation events were rare, resulting in a relatively stable population. After a taxon persisted for 25 generations, the extinction rate probability of extinction increased rapidly as shown by the very steep slope for durations of 25 through 40 generations. This increase in slope occurred because under relatively stable fitness conditions, the total population grew old as a unit. In this particular case, age and time are almost coincident, and the age axis can be thought of as a time axis. After approximately 20 generations had passed, competition had finally reduced the number of individuals in the less favored groups to the

point where extinctions began to occur. Whenever species density is reduced by extinction, speciation probability increases. As new species appeared, some of their locations in fitness space placed them in more favorable survival positions. This tended to increase competition and cause the extinction of some of the longer-lived groups.

The other survivorship curves in Figure 5 illustrate conditions of higher extinction rates throughout the entire run. DSURV values of .005 and .008 produce more intense competition between species, and speciation and extinction are common events. The tendency toward constant survivorship observed in curves II and III occurs because there is no waiting period for competition to reduce the number of individuals in the less favored species to the extinction level. Competition is high enough to reduce numbers rapidly, and many groups are near extinction levels after surviving only a few generations. As soon as extinction occurs, probability of speciation increases and a static equilibrium is established. The trend toward increasing concavity with increasing competition suggests that species with durations greater than some minimum duration (where the curve becomes sub-parallel to the duration axis) have an increased probability of avoiding extinction, whereas those with shorter taxonomic durations have a higher probability of extinction.

Because studies of taxonomic survivorship remove the

temporal effects and concentrate on age-related evolutionary processes, it is important to note that indirectly, temporal processes still influence survivorship patterns in specific cases. We would normally look to intrinsic age-related factors for explanation of survivorship trends, but this additional source of information must be considered, together with biases inherent in sampling the fossil record.

If the patterns shown in Figure 5 have general application to fossil and living taxa, it is possible that unstable taxonomic groups undergoing changes in survival potential tend to produce taxonomic survivorship curves with higher slopes and more nearly constant mean rates of extinction. Stable groups tend to exhibit non-linear survivorship curves because new taxa have a higher probability of successfully claiming their share of the resources. This is shown by the flat-topped upper portion of the survivorship curve observed under stable conditions. If the time axis were used instead of duration, the flat portion of the curve would represent a period of static conditions during which extinctions were low-frequency events, followed by a time of more frequent extinctions as competition effects reached levels necessary to produce dynamic population conditions. It is apparent that a simple change in one input variable produces widely different results. Because these changes are reasonable, an indirect check on the operation of the simulation model is provided.

Survivorship curves show changing survivorship with taxonomic age but do not give a temporal picture, except in the situation where time and taxonomic age happen to correspond. To better represent changes through time, Figure 6 is a plot of the per-cent of total extinctions occurring in eight consecutive five-generation time periods. The approximate constancy of the extinction rate through time for the high competition situation can be contrasted with the extreme variability in the extinction/ time for the low competition boundary conditions. Cladograms can also be plotted to show the temporal development of taxonomic groups. Figure 7 is a series of cladograms, with numbers 1 - 5 produced under conditions of low competition(.001), and numbers 6 - 10 produced under high competition(.008). Several general observations can be made. The low-competition conditions produce no activity for over half of the run, and then only very conservative diversification occurs. In the high-competition situation, diversification and extinction occured after only a few generations. Then one very successful group became dominant for the remainder of the run. The high-competition conditions allowed one well-positioned group to gain control of the resources (fitness space) early in the run, and all further diversification and extinction occured within this monophyletic group.



Figure 6. Temporal pattern of extinction for high(DSURV = .003) and low(DSURV = .001) competition.





Effect of Resource Instability

Stability of nutrient supplies is an important factor determining the spatial diversity patterns in modern environments (Valentine, 1971; Valentine and Moores, 1974). In the simulation, resource instability was modeled by changing the degree of variability in the fitness position. Inherent in the model design were factors which did not allow diversity to respond to conditions of resource stability as predicted by analysis of natural systems. No systematic results for this series of runs were obtained. In general, by the time resource instability had reached the point where it should be expected to produce systematic changes in taxonomic survivorship, welladapted taxa had control of resource space and resource instability did not disrupt their diversification. This result is considered to be an artifact of the model design, rather than a significant result which should be applied to diversity interpretation.

## Effects of Changes in Area

The effects of changes in the availability of resources were discussed in the methods section. The saturation number of species increases as area increases, simulating an increase in resources and a concomitant increase in diversity. A direct analogy could be drawn to opening of previously uncolonized zones in the natural environment. New resources become available

and the diversity and abundance of life adjusts to the new resource situation.

Survivorship curves for conditions of increasing area (I) and decreasing area (II) are shown in Figure 8. DSURV was set at .002 in both runs so that competition effects would not override the effects of systematic changes in area. Curve I shows a constant age-specific survivorship in a situation where area is systematically increasing by 1% per generation for 40 generations. Curve II displays a lower extinction rate for durations of less than 16 generations. For taxonomic durations of greater than 16 generations, the extinction rate increased to values near those of Curve I. The lower slope for durations less than 16 generations is the result of the same general situation discussed in the competition section. For approximately 16 generations, although area was decreasing by 1% per generation, speciation and extinction events did not produce much turnover in the population. After the original group of taxa had survived 16 generations, decreasing area and differential reproduction rates caused an increase in the rate of extinction. In Curve I, the higher and relatively constant slope is attributable to the adjustment of extinction and speciation rates to dynamic conditions of resource increase. The high extinction rate for taxa of short durations reflects the conditions of rapid turnover. Because decreasing area is limiting speciation, extinction occurs only when competition reduces the older well-established species



Figure 8. Survivorship curves for conditions of increasing(I) and decreasing(II) area (resources).

to extinction level under Curve II conditions. Temporal extinction patterns for the two runs are shown in Figure 9. In addition, representative cladograms from each of the runs are displayed in Figure 10. The cladograms are very different for the two sets of boundary conditions: Clades 1 - 5 show various patterns of increasing diversity, with clade 1 becoming extinct just before the end of the run; Clades 6 - 10 for conditions of decreasing area are not well developed but clade 8 shows an increase in diversity at the end of the run when all other clades have become extinct.

In the Raup et. al. simulation(1973), restrictions on clade size and shape limited the potential variety of clades. The logic used in this model had no such taxonomic constraints and therefore produced clades different from their model. For example, the very successful clades (Fig. 7, # 10; Fig. 10, # 3) could not occur in the stochastic simulation, and the average clade shape (symmetrical diamond) produced by the stochastic simulation is not observed in the cladograms produced by the present model.

An informal test for correspondence between simulation output and actual diversity data can be made by utilizing the reptile cladograms, prepared by Raup and Gould(1974). These cladograms are shown in Figure 11. In an admittedly subjective fashion, the following observations have been made:



Figure 9. Temporal extinction patterns for taxa plotted on survivorship curves in Figure 8.





Figure 11. Diversity variation in 17 reptilian clades (from Raup, et. al., 1973).

- 1. Cotylosauria
- 2. Chelonia
- 3. latipinnate ichthyosaurs
- 4. longipinnate icthyosaurs
- 5. Sauropterygia (plesiosaurs)
- 6. Placodontia
- "primitive" lepidosaurs 7.
- 8. Sauria (lizards)
- 9. Amphisbaenia (blind snakes)
- 10. Serpentes (true snakes)
- 11. Thecodontia
- 12. Crocodilia
- 13. Saurischia
- 14. Ornithischia
- 15. Pterosauria (flying reptiles)
- 16. Pelycosauria
- 17. Therapsida

- Figure 7: 1) Clades 1 and 3 are not unlike the cladogram for latipinnate icthyosaurs.
  - 2) Clade 5 shows the same general pattern as the ornithischians.
  - 3) Clade 8 displays a pattern similar to the cotylosaurs.
  - 4) Clade 9 is similar to the cladogram for pelycosaurs.
- Figure 10: 1) Clade 1 is more symmetrical than any of the reptile cladograms.
  - 2) Clades 2, 4, and 5 are similar to the clades for the Serpentes (true snakes) or the ornithischians.
  - Clades 6 10 do not diversify to any extent, except for clade 8 which exhibits a pattern similar to the cladogram for Sauria (lizards).

Survivorship Curves for Living and Extinct Taxa

In initial presentations of taxonomic survivorship curves by Van Valen(1973), living and extinct taxa were plotted separately. Raup(1975) suggested the  $l_x$  column in life tables for extinct and living samples could be summed, a procedure which eliminates biases toward short-lived taxa in the extinct samples, and increases total sample size.

The effect of pooling extinct and living taxa should be carefully evaluated because it can mask important information. Only in certain situations will the pooled survivorship curves retain the same slope and general shape as survivorship curves for extinct taxa. A set of survivorship curves produced by the simulation model are shown in Figure 12. Curve I is the pooled curve; Curve II is the survivorship curve for living taxa; and Curve III is the survivorship curve for extinct taxa. In this example, the difference in the age-specific extinction rates for living and extinct taxa with durations of greater than 20 generations can be observed. An example of a situation where pooling of taxa does not change the survivorship curve can be seen in Figure 4.

Analysis of Figures 4 and 12 leads to the conclusion that when total number of living taxa is small relative to the number of extinct taxa, addition of living taxa will not alter the survivorship curve, except for a slight bias toward an excess of short durations (because the living taxa have not yet reached their full durations). Because the living taxa are observed at one specific time (end of simulation), this data is a censustype record of the age-structure at one specific time in the simulation. The curve for extinct taxa is based on a record of mortality through time, similar to the fossil record. As has been shown by analysis of the boundary conditions in this model, time-related factors affect the taxonomic survivorship curves for extinct taxa, and those factors will not be recognized in census-type data for a particular "slice" through time.



Figure 12. Survivorship curves for pooled, living, and extinct samples.

**Results of Linearity Tests** 

Visual inspection of cumulative frequency curves is not a reliable means for establishing the constancy of the underlying process. Earlier discussions established the Epstein Total Lives Test as a reasonable means for statistically detecting departures from linearity. This procedure was used to test the survivorship curves produced by the simulation model. Curves shown in Figure 5 are all non-linear, according to the Total Lives Test. Curves II and III appear linear but the Epstein test specifically designed to detect too many early failures indicates the underlying distribution is not exponential because of an excess of short-lived taxa.

The survivorship curves for increasing and decreasing area (Figure 8) were tested for linearity. Under conditions of increasing area, the extinction rate is constant at the .05 confidence level. For the survivorship curve reflecting decreasing area, the test detected a nonlinear extinction rate at the .05 confidence level. Under the same boundary conditions with constant area, a general run was nonlinear.

Comparisons between simulated survivorship curves and Van Valen's taxonomic data is difficult because of the nature of his survivorship curves. However, several observations were made which could provide the basis for further investigation:

- 1) The genus level survivorship curve for extinct Pelecypoda (Van Valen, 1973, p. 3) is closely approximated by Curves II and III on Figure 5 in this paper. These are the survivorship curves for intermediate and high competition (DSURV = .005 and .008), and reflect dynamic extinction-speciation conditions throughout the runs. The similarity could be due, in part, to the instability of the environment normally occupied by clams and oysters. Because they generally live in shallow water or infratidal zones, instability in the areal extent and chemical conditions in these environments could be responsible for their high taxonomic extinction rate.
- 2) The extinction patterns produced by low competition (Figure 5, Curve I) are closest in character to the survivorship curves for extinct Foraminifera families (Van Valen, 1973, p. 2), or the curve for extinct species of Cenozoic planktonic Foraminifera(same reference). The general habitat of foraminifera tends to be more stable, and foraminifera are more mobile than pelecypods. Both of these factors cooperate to produce survivorship curves which reflect lower competition and a less dynamic taxonomic history.

3) For conditions of decreasing area(Figure 9, Curve II), the survivorship curve most closely resembling the simulated curve is the curve for extinct families of non-teleost Actinopterygii(Van Valen, 1973, p. 5). Several other vertebrate groups (extinct families of Osteichthyes; extinct genera of Edentata) show the same deviations in extinction rate during their taxonomic history. This may be a coincidence, but it could also be the result of the occasional appearance of new competitive groups during the life history of the taxa, or periods of diminishing resources during climatic change.

The curve for increasing area(Figure 9) follows the same general pattern as the curve for decreasing area, except for a flattened portion at the upper end. The curve, given by Van Valen for extinct Zoantharia families(p. 8) appears to follow the same general pattern, as does the Family level Pelecypod survivorship curve. Both of these groups exhibit changes in extinction rates from low when the group was taxonomically young, to a higher rate at the end of their taxonomic ranges. The increase in extinction rates could reflect increased competition, perhaps the result of a period of relaxed selection pressure (increasing resources) which allowed many varied phenotypes to survive.

Although the previous discussion is not highly technical or quantitative, it provides an insight into the interpretation of survivorship curves for extinct taxa. Patterns of taxonomic survivorship are the result of the interaction of the forces of selection with the evolutionary potential of the group. Mass extinction due to catastrophic events, and other time-dependent processes contribute to the patterns observed. For these reasons, interpretation of taxonomic survivorship curves requires the accumulation of detailed information regarding the fossil record of the group in question. The additional problems of monographic biases must also be considered when analysis of fossil and living taxa is attempted.

## AREAS FOR FURTHER STUDY

Simulations are designed to allow flexibility in the nature of the underlying assumptions and the degree of operator control. For this reason, it will be possible to adapt the model for investigation of other aspects of evolutionary processes. During the course of this study many potential directions of investigation were considered. Some of the more promising areas for future research are listed below:

- 1) How do rates of evolution in asexual and sexual populations compare?
- 2) The question of the relationship between genetic variability and environmental stability was briefly addressed in this paper. Recent work by Ayala, et. al.(1975) suggests stable environmental-resource conditions may foster high genetic variability in resident organisms. The importance of phenotypic plasticity should be investigated in detail.
- 3) The nature of speciation is another area deserving study, specifically that change is concentrated within the speciation event(Stanley, 1975). The different modes of speciation could be modeled, and patterns of survivorship and evolution under the various models could be analyzed.
- 4) Mayr(1963) suggested that when a species becomes highly canalized, it is less likely to survive a period of climate-resource instability. Genetic variability provides long-term protection against the agents of extinction(Stanley, 1975). Are these age-dependent effects which influence the probability of extinction of a taxonomic group?

SUMMARY

The results of this study indicate that a relatively simple model, with minimal biological constraints, can provide insight into the operation of temporal and spatial evolutionary processes. As has been succinctly stated by Kitts(1974), a model is based upon a set of general and particular preconceptions which not only influence model design, but also the manner in which "real world data" is interpreted. This raises a methodological problem, resulting from the use of "real world data" for testing simulation results. Method of treatment of empirical data may impart patterns and regularity which, in fact, do not exist. However, by analyzing simulation output within the same basic framework, it is possible analgous order will be imposed upon simulation output during interpretation.

With the previous disclaimer clearly stated, the following set of summary statements are presented:

- 1) Relatively constant taxonomic extinction rates were observed under conditions of dynamic evolutionary change in simulated lineages.
- 2) Stable, non-dynamic conditions tend to produce concavity or convexity in the survivorship curves, due to long time spans with reduced or increased extinction rates.

- 3) Both (1) and (2) represent external temporal factors which modify taxonomic duration patterns; this suggests analysis of age-related survivorship patterns requires removal of temporal effects.
- 4) Pooling of living and extinct taxa can cause substantial alteration in the survivorship curves. Living taxa are biased toward short durations, and may not contain the temporal-induced effects apparent in durations of extinct taxa.
- 5) Removal of the taxonomic restraints on lineage shape and size contained in the Raup, et. al. model(1973), and the inclusion of deterministic as well as stochastic components, produced cladograms which are not the result of preconceived notions of phylogenesis. The general cladogram shape, however, appears reasonable within the framework of the fossil record, and with the exception of the "equilibrium clade", similar to those produced by the Raup simulation.
- 6) The general model of constancy of taxonomic extinction rates cannot be accepted or rejected. A general conclusion that temporal ecological variability affects rates of taxonomic extinction within simulationproduced lineages is justified. In addition, it is probable that all three survivorship curve shape families can be found in the fossil record, dependant upon the taxonomic level which is studied. Some of the factors considered in this study are unlikely to cause modifications at the higher taxonomic levels (phylum, class, order) but would be apparent in lowerlevel taxonomic groups.



APPENDIX A



## FLOW CHART FOR EVOLUTIONARY MODEL



















Training an







APPENDIX B

## APPENDIX B

PROGRAM REPRO (INPUT, OUTPUT, TAPE60=INPUT, TAPE61=OUTPUT)

PROGRAM REPRO (INPUT, OUTPUT, TAPE60= INPUT, TAPE61=OUTPUT) 1 DIMENSION X(200), Y(200), CORX(200,27), CORY(200,27), CORZ(200,27) 2 DIMENSION AVEVAR(200), CLASS(30), CANON(200), Z(200) 3 Ă. DIMENSION POST(27), DSPEC(200), DIST(200), DISTS(200), AGE(200) DIMENSION POSIT(200), SPEC(200), SURV(200), OCCUP(20), DISWS(27) 5 DIMENSION NIND(200), OLDSPC(200.27), SPECIE(200.27), PAR(200) 6 7 DIMENSION NINDS(200) DIMENSION PAREAT(2), GENX(2), GENY(2), GENE(2), ICLAS(3,3,3) 8 DIMENSION 1x(27), Jx(27), IY(27), JY(27), JZ(27), JZ(27), DISTWS(2 9 12 17) DIMERSION CTN(100) 11 A INTEGER OFFSPG, BIGAGE 12 . REAL NICSAT, MAXVAR, NEWDIS 13 A C 14 . C..., NSPEC IS THE TOTAL NUMBER OF SPECIES, NGEN IS THE NUM C..., GENERATIONS THE PROGRAM WILL RUN. SPECIE(1, J) IS THE NGEN IS THE NUMBER OF 15 16 C.,., CLASS DESIGNATION FOR THE 27 CLASSES - CONSISTING OF EITHER CLOSED 17 C ... CLASSES, OFEN CLASSES, OR LETHALS. THE OPEN CLASSES INITIALLY 18 . C ... HAVE BO INDIVICUALS DISTRIBUTED EQUALLY ACHOSS THEN. 19 C,... ICLAS IS THE VARIABLE WHICH CONTAINS THE CLASS DESIGNATIONS FOR 20 . C..., EACH OF THE CLASSES. THIS INFORMATION IS USED TO LOCATE THE C..., POSITION IN THE 3 X 3 X 3 SPACE. THE VALUE IS EITHER 1 OR 0, C..., ACCORDING TO THE LARELING SCHEME USED, AND THE RELATIVE POSITION C..., IN SPACE. DSPACE IS THE DIMENSIONS OF THE SPACE IN WHICH THE . 21 22 . A 23 24 C..., SPECIES CENTERS ARE LOCATED. XUVIT, YUNIT, AND ZUNIT ARE THE C..., INCREMENTS OF DSPACE. CLDIST IS THE MINIMUM SEPARATION 25 . 26 C..., ALLOWED IN SPACING OF SPECIES CENTERS. C..., X(1), Y(1), Z(1) ARE THE COOPDINATES OF THE SPECIES CENTER FOR 21 28 ۸ C..., SPECIES I, STDX, ENVX, ETC. ARE THE COORDINATES AND STANDARD C..., DEVIATION FOR THE POSITION OF THE FITNESS OPTIMUM. THEY ARE 29 A se A C..., USED TO GEFERATE THE NORMAL CURVE WHICH IS USED TO RANDOMLY C..., PRODUCE NEW FITNESS OPTINUM POSITIONS. 31 A Š2 A C..., XSEL, YSEL, ESEL ARE THE VALUES USED FOR DIRECTED MOVEMENT OF THE C..., FITNESS OPTIHUM POSITION, STHULATING DIRECTIONAL MOVEMENT OF Š3 A A 34 C.... THE ENVIRONMENT (FITNESS OPTIMUM). Ś۵ A U..., ARFA, DAREA, AND NAREA ARE USED TO CONTROL THE SPECIES DENSITY. 36 37 С A 38 READ 101, IRANF, MINNO, DSURV, AREA, DAREA, NAREA A READ 182, MIRECT, STOX, ENVX, STOY, ENVY, STOE, ENVE 39 A 103, NSPEC, USPACE, XUNIT, YUNIT, ZUNIT, CLDIST 42 READ A 41 READ 104, XSEL, YSEL, ZSEL A READ 1P5, NGEN, VX1, VX2 ٨ **4**2 **4**3 READ 106, (SPECIE(1, J), J=1, 27) A AVSUR . 25 ā4 ٨ ٩S NI-0PS=30 46 CO 1 I=2,NSPEC . 41 00 1 J=1,27 A ã H SPECIE(I,J)=SPECIE(1,J) ٨ 1 49 DO 2 I=1,NSPEC A 2 CONTINUE A 50


| _        | READ 107, (1x(1),Jx(1),Iy(1),Jy(1),IZ(1),JZ(1),I=1,27)<br>READ 108, (((ICLAS(1,J,K),K=1,3),J=1+3),I#1+3)                  | A           | 71<br>72             |
|----------|---|-------------|----------------------|
| с<br>С   | RANDOM NUMBER GENERATOR FOLLOWS.  | Â           | 73<br>54             |
| C        | CALL RANSET (FLOAT (IRANF))   | Â           | 22<br>26             |
|          | DU 3 HM=1,NSPEC<br>NIND(HH)=60<br>NIND(HH)=75   | Â           | 7/<br>58             |
| -        | LANUN (MA) #/2<br>NSPECP=44   | Â           |                      |
| C J      | CONTINUE  | Â           | 02                   |
| C        | COURDINATES FOR SPECIES CENTERS, AND DISTANCE BETWEEN EACH<br>PAIR OF SPECIES ARE CALCULATED IN THE FOLLOWING STATEMENTS, | Â           | 03<br>64             |
| C        | DIS IS THE DISTANCE BETHEEN EACH SPECIES PAIR.  | Å           | 0)<br>00             |
| C        | CO 6 I=1,NSPEC  | Â           | 60<br>20             |
| 4        | CONTINUE<br>DISTANCE  | Â           | 7 B                  |
|          | R2=RANF(-1)<br>R3=RANF(-1)  | Ā           | /2                   |
|          | TR1=R1=(DSPACE=3)+2<br>TP2=R2=(DSPACE=3)+2  | Ā           | )4<br> }4            |
|          | 1R3=R3+(DSPACE-3)+2<br>x(1)=1R1+xUNIT   | Ä           | )6<br>)7             |
|          | Y(1)=1R2+YUNIT<br>Z(1)=1R3+ZUNIT  | Â           | 78<br>19             |
|          | IF (I.EQ.1) GO TO 6<br>JMAX=I-1   | A           | <u>0</u> 0<br>01     |
|          | DIS=((X(I)=X(J))++2+(Y(I)=Y(J))++2+(Z(I)=Z(J))++2)++3   | A           | 82<br>83             |
| C,<br>C, | DIS LESS THAN CLDIST SPECIES IS NOT ALLOWED IN THIS<br>Position, Relocate this species.                                   | A<br>A<br>A | 84<br>85<br>85<br>87 |
| L        | IF (DIS.GT,CLDIST) GO TO 5<br>GO TO 4   | Ā           |                      |
| 5        | CONTINUE  | Ä           | 99<br>91             |
|          | DO 10 I=1,NSPEC<br>J=0  | Â           | 92<br>93             |
|          | DO 9 II=1,3<br>DO 8 JJ=1,3  | Å           | 94<br>95             |
|          | DO 7 KK=1.3<br>J=J+1  | Å           | 96<br>97             |
| C<br>C   | FOLLOWING STATEMENTS CALCULATE COONDINATES FOR 27 CLASSES,<br>These class positions are fixed after species center        | A<br>A<br>A | 78<br>99<br>198      |

PROGRAM REPRO (INPUT.OUTPUT.TAPE68-INPUT.TAPE61-OUTPUT)

| C        | HAS BEEN LOCATED.   |          | 191   |
|----------|---|----------|-------|
| C        |   |          | 102   |
|          | CORX(I,J)=(X(I)-XUNIT)+(II-1)+XUNIT                             | A        | 103   |
|          | CORY(I,J) = (Y(I) - YUNIT) + (JJ - 1) = YUNIT                   | A        | 104   |
|          | COR7(1.J) - (7(1) - 7UNIT) . (KK_1) - 2UNIT                     |          | ĨġS   |
| 7        |   | Â        | 106   |
| á        |   |          |       |
|          |   |          | 10/   |
| 9        | CONTINUE  |          | 100   |
| 10       | CONTINUE  |          | 109   |
| C        |   | A        | 118   |
| ċ        | IN LOOP IS THE GENERATION LOOP                                  |          | 111   |
| <b>c</b> |   |          | 112   |
| C I      |   |          | 113   |
|          | DO DO IMETINOEN   | <b>.</b> |       |
|          | PRINT 109, IF   |          | 142   |
| C        |   | A        | 117   |
| C i      | JM LOOP TAKES SPECIES THROUGH REPRODUCTION AND CANALIZATION     | A        | 116   |
| c        |   |          | 111   |
| •        | DD 37 IM-1.NSPEC  | Ā        | 118   |
|          | JU J/ JHEIMALES 78 44   |          | 1 9 9 |
|          | IF (4100 SP)/ 3/13/11   |          | 11    |
| 11       | CONTINUE  |          | TEB   |
|          |   | •        | 121   |
|          | Keð   |          | 122   |
|          | DD 13 J=1+27  |          | 123   |
|          | OUDSPC(JH.J)=SPECTE(JH.J)                                       | Â        | 124   |
|          |   | -        | 125   |
| 4.2      |   |          | 126   |
| 14       |   | 2        | 120   |
|          | PAH (K) = SPECIE (Jn ; J)                                       |          | 14/   |
|          | GLASS(K)=J  | A        | 129   |
|          | SPECIE(JM,J)=3  | A        | 129   |
| 13       | CONTINUE  | A        | 1 3 0 |
| r -      | • • •   |          | 131   |
| č.       | THE FOLLOWING STATEMENTS ARE THE CANALIZATION PORTION OF THE    | Â        | 132   |
|          | PROCEAN USED ONLY IN THE SECOND MODE OF OPERATION (MODE 11)     |          | 1.3.3 |
|          | WICH A OFFICE IS WITHIN A FIVE DISTANCE OF THE STINESS          | 2        | 134   |
| C        | WHILE A STELLES IS WITHIN A FIALD DISTANCE OF THE FINESS        | <u></u>  | 104   |
| C        | OPTIHUM FOR A PRESET NUMBER OF TIERATIONS, THE NUMBER OF CLASS  |          | 199   |
| C        | AVAILABLE FOR OCCUPATION IS DECREASED, THIS IS AN ATTEMPT TO    |          | 130   |
| C        | SIMULATE THE DEVELOPMENT OF SPECIALIZED FORMS(PHENO AND GENO)-  | A        | 137   |
| C        | AND SUCCESTS THAT STABLE RESOURCE CONDITIONS HAY PRODUCE A      |          | 138   |
| <b>C</b> | DECUEACE IN GENETIC VADIABILITY AS PROPOSED BY BRETSKY          |          | 139   |
| <u> </u> | AND LOCK TO CARLEND VERIALIZITY OF PROPOSED OF DREPORT          | Ā        | 140   |
|          | AND LUNEATENTIAL TO THE NATURE OF THE LINK SETHERN BUENALYRE    | Ξ.       | 141   |
| G        | THE OUESTION AS TO THE NATURE OF THE LINK BETWEEN THENDITE      | Å        | 147   |
| C        | AND GENOITPE MUST HE ANDRESSED. IF THE LINK IS ASSUMED TO BE    |          | 746   |
| C        | DIRECT, THEN CHANGES AT THE PHENOTYPE LEVEL IN RESPONSE IO      | A        | 143   |
| C        | SELECTION PRESSURE WILL HAVE IMMEDIATE EFFECTS AT THE GENOTYPE  | A        | 144   |
| C        | LEVEL. IT IS POSSIBLE, HOWEVER, THAT THE MORE COMMON            | A        | 145   |
| <u> </u> | STTUATION IS THAT ALTHOUGH PHENOTYPIC VARIABILITY               |          | 146   |
| ~        | DECHEASES, THE CENETIC VARIADII ITY IS MAINTAINED DUE TO THE    | Ā        | 147   |
|          | DEVELOPMENT OF GENELIZED TOATTE AND CHARACTER COMPLETES         | ~        |       |
| U        | UEVELUMENT OF GANALIEU INALIS AND CHANAGIER COMPLEXES           |          | 170   |
| C        | A THIND ALTERNATIVE IS SUGGESTED BY VALENTINE AND ATALA (1975). | A        | 127   |
| C        | THEY PROPOSE THAT A SPECIES IN STABLE RESOURCE CONDITIONS IS    | A        | 120   |

| C          | HORE LIKELY TO EXHIBIT HIGH VARIABILITY DUE TO HANY HAYS TO   | A 171 |
|------------|---|-------|
| C          | MAKE A SUCCESSFUL LIVING. TOTAL DATA IS INCONCLUSIVE.         | A 172 |
| C          |   | A 173 |
|            | IF (CANON(JH)+LT+75) GO TO 20                                 | A 154 |
|            | IF (CANON(JH).E0.76) GO TO 14                                 | A 175 |
|            | IF (CAPON(JH).EQ.77) GO TO 15                                 | A 156 |
|            | IF (CANON(JH) + EQ + 78) GO TO 16                             | A 157 |
|            | IF (CANON (JH) + EQ + 79) GO TO 17                            | A 158 |
|            | IF (CANON(JH).EQ.60) GO TO 18                                 | A 179 |
|            | IF (CANON(JM).EQ.81) GO TO 19                                 | A 100 |
|            | G0 Y0 20  | A 101 |
| 14         | OLDSPC(JM+1)=-1   | A 102 |
|            | 0LDSPG(JM;27)=-1  | A 103 |
|            | 0LDSPC(JM+7)=-1   | A 107 |
|            | 0[USPC(JM+21)=-1  | A 105 |
|            |   | A 100 |
| 12         |   | A 10/ |
|            |   | A 100 |
|            |   | A 107 |
|            |   | A 1/0 |
| 4.6        |   |       |
| 10         |   | A LIE |
|            |   | A 1/3 |
|            | 0[0506(]0120]=1   | A 1/7 |
|            |   | A 1/6 |
| 17         |   |       |
| <b>*</b> ' |   |       |
|            |   | A 1/0 |
|            |   | A 188 |
|            |   | A 181 |
| 18         |   | A 182 |
| •••        | $0   \cup SPC( \cup M + 18) = 1$                              | A 183 |
|            | 0LDSPG(JM:12)=1   | A 184 |
|            | 0LDSPC(JM+16)=-1  | A 185 |
|            | 02 07 00  | A 186 |
| 19         | CLDSPC(JM+13)=-1  | A 167 |
|            | 0LDSPC(J <sup>1;</sup> ,15)=-1                                | A 198 |
| 20         | CONTINÚE  | A 189 |
| 21         | CONTINUE  | A 198 |
| С          | _   | A 191 |
| C          | POTENTIAL PARENT CLASSES ARE ISOLATED, IF GENOTYPE AND        | A 192 |
| C          | PHENOTYPE WERE NOT DIRECTLY RELATED, ALL CLASSES COULD ACT AS | A 173 |
| C          | PARENTS, THIS WOULD ALLOW HIGHLY GANALIZED SPECIES TO         | A 194 |
| C          | UTILIZE THEIR INHERENT VARIABILITY AS MAYR(1963) SUGGESTS     | A 175 |
| 6          | THEY ARE ABLE TO UD.  | A 190 |
| <b>U</b>   | TWO PARENTS ARE CHOSEN FOR REPRODUCTION                       | A 17/ |
| U I        |   | A 140 |
|            | UU 24 NH1/2<br>D4-D4-N5/-4-1                                  | A 177 |
|            | N9=NAN( \"1)  | v cåa |

A 201 IRAND=R4+(NIND(JM)-1)+1 ¥ 505 SUM=P. A 203 K=(j A 204 22 K=K+1 A 205 SUM=PAR(K)+SUM A 206 C WHEN IRAND IS LESS THAN SUN, PREVIOUS CLASS CONTAINS A 207 C.... C . . . . THE INDIVIDUAL PAR(K). A 208 С A 209 IF (1RAND-SUM) 23,23,22 A 218 С A 211 FOLLOWING STATEMENT IDENTIFIES PARENT AS BEING FROM CLASS K. A 212 C..., A 213 C 23 PARENT(N)=CLASS(K) A 214 A 215 24 CONTINUE A 216 111=0 A 217 111=4 A 218 KKK # 3 A 219 С THE 68 LOOP COMBINES PARENT GENOTYPES RANDOMLY TO PRODUCE A 228 C.... C..., THE OFFSPRING GENOTYPE. A 221 С A 222 A 223 00 34 N=1,2 A 224 C A 225 C... PARENT(N) IS THE CLASS TO WHICH PARENT N BELONGS. A 226 С INT=PARENT(N) A 221 A 228 С INT RUNS FROM 1-27 IX, IJ, ETC, ARE READ IN AND ARE THE CLASS NOTATIONS FOR A 229 C . . . . A 238 C . . . j A 231 CLASSES 1 - 27. C.... A 232 С A 233 X1=IX(INT) A 234 X2=JX(INT) A 235 Y1=IY(INT) A 230 Y2=JY(INT) A 231 21=17(INT) A 238 72=J2(INT) A 239 С IF IX AND JX ARE THE SAME VALUE, GENL X IS GIVEN THIS VALUE, SIMULATING THE HOMOZYGOUS STATE. IF IX AND JX ARE UNEQUAL, A RANDOM NUMBER IS CHOSEN. IF THE RANDOM NUMBER A 248 C... A 241 C . . . . A 242 C . . . . IS LESS THAN .5. THE X1 VALUE IS ASSIGNED A 243 C... A 244 TO GENE X. C.... IF THE RANDOM NUMBER IS GREATER THAN .5, THE X2 VALUE IS A 245 C..., ASSIGNED TO GENE X. LIKEWISE FOR GENES Y AND Z. A 246 C . . . . A 247 C..., A 248 A 249 С IF (X1.E0.X2) GO TO 26 RX=RANF(-1) A 25E

|             | 15 (RX.6T 5) 60 TO 25  |          | 251        |
|-------------|--|----------|------------|
|             | GF F W = X 1   | - î      | 252        |
|             |  | - 7      | 253        |
| 25          |  | <b>.</b> | 254        |
| 21          |  | •        | 227        |
| - <i>i</i>  | 60 10 2/   |          | 522        |
| 20          | GE VEX #X1   | A .      | 520        |
| 27          | CONTINUE   |          | 227        |
|             | IF (Y1.EQ.Y2) GO TO 29   | A        | 228        |
|             | RX=RANF(-1)  | A        | 259        |
|             | IF (PX,GT,.5) GO TO 28   | A        | 208        |
|             | GENEY#Y1   |          | 201        |
|             | GO TO 30   | Â        | 262        |
| 28          | GENEVAY2   | Â        | 283.       |
| • •         |  | <b>.</b> |            |
| 20          |  | - 7      | 525        |
| 27          |  | •        |            |
| 30          |  |          | 200        |
|             | IF (21.E0.22) GO TO 32   | A        | 20/        |
|             | RX3RANF(+1)  | A        | 200        |
|             | IF (PX,GT, 5) GO TO 31   | A        | 508        |
|             | GENEZ=21   |          | 278        |
|             | GO TO 33   |          | 2/1        |
| 31          | GENEZ=Z2   | A        | 2/2        |
| -           | GO TO 33   | A        | 213        |
| 32          | GFUF7#Z1   |          | 214        |
| 33          | COUTINUE   | Â        | 2/5        |
| r           |  |          | 216        |
| ř.          | VALUES FOR GENE V. GENE V. AND GENE & HAVE REEN ORTAINED.  |          | 212        |
| ~ · · · · · | ALTER OF ALTER AT BEAC AT AND BEAC - HAVE BEEN BOTH THEY   |          |            |
| L           |  | -        | 2/0        |
|             |  | •        | 217        |
|             |  |          | C 8 C      |
| _           | GENE (N) = GENEZ   | <b>A</b> | 201        |
| <u>c</u> .  |  | A .      | 565        |
| C.,.,       | PREVIOUS THREE STATEMENTS STORE GENUIVES OF PARENT(N).   | A        | 203        |
| C           | FOLLOWING STATEMENTS SUM GENOTTPE VALUES FOR EACH COORDINATE   | A        | 284        |
| C           | SO THAT CLASS IDENTIFICATION IS POSSIBLE.  | A        | 562        |
| C           |  |          | 560        |
|             | 1 [ ] = [ ] [ + GENX (N)   | A        | 287        |
|             | JJJ=JJJ+GENY(N)  | A        | 288        |
|             | KKK#KKK+GENZ(N)  | Á        | 289        |
| 34          | CONTINUE   |          | 298        |
| -           |  | Â        | 291        |
|             |  |          | 242        |
|             |  |          | 243        |
|             | OFFSPELTELAS/III.LII KKKA  |          | 244        |
| c           | olla. Antorna (TITIAAA) www.   | <b>2</b> | 245        |
|             | TE OFFORTING TO MON-VIAN F. NEWING IT DE AND TO A STAR   | <u> </u> | 504        |
|             | IT UTISTING IS NUN-VIABLE, HEANING II DELUNGS IU A GLADS<br>Assistant A1 Brachan Devinant to Catatement A. And | Ā        | 270        |
|             | ADDIGHTER A TI, FRUCKAR KEIVKAD IN DIAIEMENI AN AND<br>Ceneditee   |          | 671<br>50# |
|             | ULINERALES IND NEW PARENIS .   |          | 270        |
| C           |  |          | SAA        |
|             | IF (OLDS/G(JM/OFFSPG)) 21,35,35  | A        | 246        |

| 35      | CONTINUE<br>COUNT=COUNT+1<br>SPECIE(JM,OFFSPG)=SPECIE(JM,OFFSPG)+1  | A<br>A<br>A | 341<br>342<br>343 |
|---------|---|-------------|-------------------|
| с<br>С, | PREVIOUS STATEMENT SUMS NUMBER IN OFFSPRING CLASS   | A           | 305               |
| c ·     | 1F (COUNT.LT.NIND(JH)) GO TO 21   | Â           | 300               |
| Č,<br>C | RETURN TO BEGINNING OF REPRODUCTION FOR SPECIES 2.  | Â           | 309<br>310        |
| 74      | DO 36 J=1,27<br>IF (OLDSPC(JH,J).EQ1) SPECIE(JH,J)=-1   | A           | 311<br>312        |
| 37      | CONTINUE<br>Continue<br>IF (direct.LT.2) GO TO 38   | Å           | 313<br>314<br>315 |
| с<br>С, | THE NORMAL SUBROUTINE IS USED TO MOVE THE FITNESS OPTIMUM.  | A<br>A      | 316<br>317        |
| C       | ME COURDINATES OF THE PREVIOUS FITNESS FUSITION ARE USED AS<br>MEAN VALUES, AND STANDARD DEVIATIONS ARE READ IN. THE MOVEMENT<br>OF THE FITNESS POSITION WILL BE PROBABILISTIC, WITH THE MOST | Â           | 319<br>320        |
| C,<br>C | PROBABLE HOVE A SHALL ONE FROM THE PREVIOUS POSITION.   | Â           | 321<br>322        |
|         | CALL NORMAL (ENVX,STDX,EX1)<br>CALL NORMAL (ENVY,STDY,EY1)<br>CALL NORMAL (ENV2,STD2,E21)   |             | 323<br>324<br>325 |
| С       | GO TO 39  | Â           | 526<br>521        |
| C,      | FOLLOWING STATEMENTS ALLOW DIRECTIONAL MOVEMENT OF<br>Fitness optimum position.   | A           | 328<br>329<br>338 |
| 38      | ENVX=ENVX+XSEL<br>ENVY=ENVY+YSEL  | Â           | 331<br>332        |
|         | ENV7=ENV7+ZSEL<br>EX1=ENVX  | A           | 333<br>334        |
| 29      | EY1=UNVY<br>EZ1=ENVZ<br>CONTINUE  |             | 335               |
| J.      | PRINT 110, EX1, EV1, EZ1<br>ENVX=EX1  | Â           | 338               |
|         | ENVY=EY1<br>ENVZ=E21<br>M=0   | A           | 348<br>341<br>342 |
| C       | FOLLOWING LOOP GALCULATES AVERAGE AND MAXIMUM VARIANCE  | Â           | 343<br>344        |
| C       | FOR SPECIES FOR USE IN CALCULATING SPECIATION PROBABILITY.  | A           | 395<br>340<br>347 |
| 4 -     | DO 45 1=1,NSPEC<br>1F (NIND(1)) 45,45,40  | Ä           | 348<br>349        |
| 9 8     | K BK +J   |             | 378               |

| SPEC(K)=1   | A 371                |
|---|----------------------|
| <b>ປ</b> ະຄິ  | Ä 352                |
| SX=3  | A 353                |
| SY=0  | A 354                |
| SZ=0  | כנ A                 |
| SUHX2=0   | 6¢6 A                |
| SUMY2=P   | A 35/                |
| SUM22=0   | 855 A                |
| D0 42 J=1,27  | A 379                |
| IF (SPECIE(I,J)) 42,41,41   | A 368                |
| 41 SX=SPECIE(I,J)+CORX(I,J)+SX  | A 301                |
| SY=SFECIE(I,J)=CORY(I,J)=SY   | A 362                |
| SZ=SPECIE(I,J)+CORZ(I,J)+SZ   | ¥ 203                |
| 42 CONTINUE   | A 304                |
| XBAR=SX/NIND(I)   | A 365                |
| YBAR=SY/NIND(I)   | A 366                |
| ZBAR=S7/NIND(I)   | A 307                |
| 00 44 J#1,27  | A 308                |
| IF (SPECIE(I,J)) 44,43,43   | ¥ 204                |
|   | A J/B                |
| TULY=CURT(I)J)=TUAR<br>ZUCV=CORT(I)J)=TUAR  | A 3/1                |
| EULY=5URE(1))=5UAK<br>EULY=5URE(1))=5UAK  | A 5/2                |
| SUM22-YDEVAYDEVASBECIE(1, J)+SUM2   | A 3/3                |
| 50 1722 DEV 0 0 0 0 57 20 1 20 1 4 30 1 4 30 1 4 30 1 4 30 1 4 30 1 4 30 1 4 30 1 4 30 1 4 30 1 4 30 1 4 30 1 4 | A 3/5                |
|   | A 3/6                |
|   | A 3/7                |
|   | A 3/8                |
| VADZESUMZZ/(NIND(I)-1)  | A 3/9                |
| SDX=SQRT(VARX)  | A SUL                |
| SDY SORT (VARY)   | A 301                |
| SP7=SORT(VARZ)  | A 382                |
| AVEVAR(1)=(SDX+SDY+SDZ)/3   | A 383                |
| DVAR=(1+VX1+AVEVAR(1)++VX2)   | A 384                |
| C   | A 385                |
| C, FOLLOWING STATEMENT CALCULATES DISTANCE BETWEE   | SPECIES CENTER A 306 |
| C, AND FITNESS OPTIMUM, DISTANCE IS STANDARDIZED  | FOR INTERNAL A 387   |
| C, SPECIES VARIABILITY BY DIVIDING BY THE AVERAGE   | VARIANCE. A 388      |
|   | A 389                |
| DISI(K)=20HI((X(I)=ENAX)==2+(4(I)=ENA4)==2+(5)  | J-LNVE/-2//UVA A 398 |
|   | A 371                |
| TE VAVENARIIN ET MAYNARN MANNARDAVENARIIN   | A 343                |
| 45 CONTINUE   | A 394                |
|   | געניי<br>געני        |
| C SORT IS A SUBROUTINE WHICH ORDERS THE DISTIKS FO  | SPECIES A JV6        |
| C PRESENT FROM CLOSEST TO FURTHEST FROM THE FITNES  | OPTINUN. A 397       |
| C   | • •                  |
|   | A JYU                |
| CALL SORT (NSPECP,DIST)   | V 3Å8<br>V 3Å8       |

|              | PROGRAM REPRO (INPUT.OUTPUT.TAPE60=INPUT.TAPE61=OUTPU])   |      |
|--------------|---|------|
|              | DO 46 KK=1,NSPECP   | A 41 |
| С            |   | A 41 |
| C            | IF THE FOLLOWING STATEMENT IS TRUE, THE KK VALUE<br>Identifies the Position of the KTH species in the sequence. |      |
| 6            | IF (DISTS(K), EQ. DIST(KK)) GO TO 47  | 4    |
| 46           | CONTINUE  | A 41 |
| 47           | POS1T(K)=KK   | A 41 |
| _            | L1=SPEC(K)  | A 4  |
| C<br>C       | POSITIVE IS THE POSITION OF COFCIES PELATIVE TO THE FITNESS   |      |
| C            | OPTIMINE TO THE POSITION OF SPECIE CANADA AND AND THE FIRE  |      |
| C            | INCREMENTED.  | A 4  |
| C            |   | A 4  |
|              | IF (POSIT(K)-10) 48,48,49   | A 4  |
| 48           | CANO!(L1)=CANON(L1)+1   | A 4  |
|              | PHINT III, SPEC(R), GANON(L1)   | A 7  |
| <b>A</b> U   | GO TO 49<br>Company   |      |
| с <b>ч</b> , | CINITNOL  |      |
| C            | FOLLOWING STATEMENTS KEEP FOULD IPPIUM NUMBER OF INDIVIOUALS  |      |
| C            | BY SETTING UPPER AND LOVER LIMITS ON THE NUMBER ALLOWED.  |      |
| C            | THE CUTRACK OR INCREASE IS NOT IMMEDIATE SINCE THE CONTROL  |      |
| C            | IS SET SO THAT WHEN THE NUMBER FALLS TOO LOW. THE SURVIVAL  | Ă    |
| C            | PERCENTAGE OF THE AVERAGE FITNESS POSITION IS INCREASED.  | Ä 4  |
| C            | THIS KEEPS THE NUMBER OF INDIVIDUALS WITHIN A RANGE OF THE  | A 4  |
| C,           | CHOSEN NUMBER,  |      |
| C            | •   | A 4  |
|              | DO 50 K=1,NSPECP  | A 4  |
|              | L1=SPEC(K)  | A 4  |
|              | NINDS(L1)=NIND(L1)  | A 4  |
| 50           | CONTINUE  |      |
|              | NIUIALSAKEANNINUPS  |      |
|              |   |      |
|              | NLUME,/JENIUIAL   |      |
|              | TINTANSPECP/2   |      |
|              |   |      |
|              | 1F (1HT.FQ.TINT) GO TO 51   | 74   |
|              | Go to 52  | 4    |
| 51           | CSPEC=NSPECP/2  | 4    |
|              | GO TO 53  | A 4  |
| 52           | CSPEC=NSPECP/2+1  | A 4  |
| C            |   | A 4  |
| C            | FOLLOWING STATEMENTS DETERMINE FITNESS OF SPECIES ASSUMING  | A 4  |
| C,           | AVERAGE FITNESS IS 29 PERCENT.  | A 4  |
| C            |   | A 4  |
| 2.1          | TIDERADURE (COMECAL) ODSURA   |      |
|              | VISNIAL<br>Duant 440 - M Avend  |      |
|              | LAINI TTC' INVAARA  | A 43 |

|     | PROGRAM REPRO (INPUT,OUTPUT,TAPE68=INPUT,TAPE61=OUTPUI)   |        |
|-----|---|--------|
|     | DO 54 KOUNTEL.NSOFCP                                      | A 451  |
|     | KSKOUNT-1   | A 452  |
| C   |   | A 453  |
| C,  | NEXT STATEMENT ESTABLISHES SURVIVAL VALUE OF EACH SPECIES | A 474  |
| C   | POSITION RELATIVE TO FITSP, THE BEST ADAPTED SPECIES,     | A 455  |
| С   |   | A 476  |
|     | KKESPEC(KUUNT)  |        |
| 54  | SURV(ROUNI) EF (ISF=(R=USURV)<br>Constants                | A 428  |
|     |   | 468    |
|     | NB1G=2  | 401    |
| С   |   | A 462  |
| C   | THIS LOOP CALCULATES THE NUMBER OF INDIVIDUALS IN EACH    | A 403  |
| C   | SPECIES PASED ON PERCENT SURVIVAL FOR THEIR POSITION.     | A 404  |
| C   |   | A 405  |
|     | 00 55 K=1,NSPECP  | A 406  |
|     |   | A 407  |
|     |   | A 400  |
|     | NINU(L1)=SURV(L2)=4=NINUS(L1)<br>SUBNI-SURVAL10(14)       | A 478  |
|     | IE (UIND(L1) GT NRIG) NRIG-NIND(L1)                       | 471    |
| 55  |   | 4/2    |
| C   |   | A 4/3  |
| Č   | FOLLOWING STATEMENTS INCREMENT PERCENT SURVIVAL BASED ON  | Ä 4/4  |
| C   | NUMBER OF INDIVIDUALS PRESENT.                            | A 4/5  |
| C   |   | A 4/6  |
|     | 1F (NT,E0,2) GO TO 58                                     | A 4/7  |
|     | IF (SUNN.LT.NLOW) GO TO 56                                | A 4/8  |
|     | IF (SUMA.GI.NHIGH) GO TO 57                               |        |
| 56  |   | A 481  |
| 20  | CO TO 53  | 482    |
| 57  | AVSUR=AVSUR=.01   | A 483  |
|     | GO TO 53  | A 484  |
| 58  | CONTINUE  | A 487  |
|     | PRINT 113, NSPECP   | A 486  |
|     | PRINT 114, SUHN   | A 487  |
|     | NO 59 KE1,NSPECP  | A 488  |
|     |   | A 407  |
|     | L2#7 J311147<br>PPINT 115. 11.NIND/(1), RUPU/(2)          | A 491  |
| 59  | CONTINUE  | 492    |
| C   |   | A 493  |
| Č   | CLASS LEVEL SELECTION FOILOWS                             | A 494  |
| C   | CLASSES WITHIN SPECIES ARE NOW ASSIGNED MEMBERS BASED ON  | A 495  |
| C,  | RELATIVE DISTANCE FROM FITNESS OPTIMUM,                   | A .496 |
| С   |   | A 497  |
|     | DO BA TAT'NEAC  | ¥ 448  |
| 4 7 | TE (NIND(T)) 08'08'08                                     | A 477  |
| 0 M | ~ = U   | V SÁR  |

|      | PROGRAM REPRO (INPUT,OUTPUT,TAPE60=INPUT,TAPE61=OUTPUI)       |     |             |
|------|---|-----|-------------|
|      | D0 62 J=1,27  | A   | 5 <b>01</b> |
|      | IF (SPECIE(I,J)) 62,61,61                                     | A   | 265         |
| 61   | K=K+1 .   |     | 262         |
| C    |   | A   | 204         |
| C,,, | OCCUP(K) RECORDS NUMBER OF INDIVIDUALS IN CLASS K.            | ٨   | 202         |
| C,   | CLASS(K) CONTAINS THE CLASSES WHICH ARE OCCUPIED.             | A   | 200         |
| C    |   | A   | 207         |
|      | $C_{L}ASS(k) = J$   | A   | 500         |
|      | OCCUP(K) SPECIE(I,J)  |     | 207         |
| 47   | SPECIE(I,J)=0   | . 👗 | 210         |
| 04   |   |     | 211         |
|      | DO 02 II-IK   | -   | 546         |
| c    | KI=CLA33(11)  |     | 210         |
|      | CALCULATE DISTANCE FOOM FACH CLASS TO ENVIRONMENTAL           |     | 515         |
| C    | OPTIMUM POSITION  | - 7 | 516         |
| C    | or 11.00 + 0011104  | - 2 | 517         |
| U U  | DISWS(11)=SQR1/(CORX/1.K1)=FNVX)=#2#(CORY(1.K1)=FNVY)+#2#(CO  | - 2 | 518         |
| 1    | $R^{2}(1, K_{1}) - F(V_{2}) = 0$                              | Â   | 519         |
| •    |   | Ā   | 520         |
| 65   | CONTINUE  | Â   | 521         |
| С    |   | A   | 522         |
| C    | CLASSES ORDERED FROM CLOSEST TO FURTHEST FROM FITNESS OPIIMUM | A   | 5Ż3         |
| C    | BY SORT,  | A   | 524         |
| C    |   | A   | 525         |
|      | CALL SORT (K,DISWS)   |     | 526         |
|      | $DO_{66} II = 1, K$   | A   | 527         |
|      | Do 64 JII=1,K   | A   | 528         |
|      | IF (DISTWS(II),EQ.DISWS(III)) GO TO 65                        |     | 529         |
| 64   | CONTINUE  | Å   | 530         |
| 07   |   |     | 201         |
| 00   | CONTINUE  |     | 552         |
|      | SUN=9<br>SUN=9  | •   | 534         |
| c    | 2045-61   |     | 535         |
| C    | FOLLOWING STATEMENTS CALCULATE NUMBER IN EACH CLASS           |     | 536         |
| 6    | AFTER SELECTION.  | Â   | 537         |
| c    |   | Â   | 550         |
| •    | D0 67 11=1.K  | Â   | 539         |
|      |   | Â   | 540         |
|      | SU12#SUM2+(POST(11)-1)+.01+0CCUP(11)+4                        | Å   | 541         |
| 67   | CONTINUE  | Â   | 542         |
| с    |   | Ä   | 543         |
| C    | CONST IS THE VALUE WHICH ASSIGNS CORRECT NUMBER OF            | Ä   | 544         |
| C    | INDIVINUALS TO EACH CLASS,                                    | A   | 545         |
| C    |   | A   | 546         |
|      | CONST=(NIND(I)+SUM2)/SUM                                      | A   | 547         |
|      | SUH=u,  | A   | 548         |
|      | SUH2=0,   |     | 549         |
|      | nd en 11=1'k  |     | 238         |

|        | PROGRAM REPRO (INPUT.OUTPUT.TAPE60*INPUT.TAPE61*OUTPU!)    |        |
|--------|--|--------|
|        | J1=C(ASS(11)   | A 531  |
|        | SPECIE(1, J1) = 4+0CCUP(11)+(CONST-(POST(11)-1)+.81)       | A 552  |
| С      |  | A 553  |
| C      | SUM CONTAINS THE NUMBER OF INDIVIDUALS IN SPECIE(I, j).    | A 224  |
| C      |  | A 555  |
|        | SUMPERSELLE(1, J1) SUM                                     | A 220  |
| 68     | CURTINIE<br>20055(255015(1191)=0502(1191)1=4562005         | A 227  |
|        |  | A 559  |
|        | DSPEC/1, SUM2  | A 568  |
| 69     | CONTINUE   | A 501  |
|        | NEXTC#0  | A 202  |
|        | DO 71 1=1,NSPECP   | A >0j3 |
| _      | L1=SPEC(1)   | A 504  |
| C      |  | A 202  |
| C      | DILUMING STATEMENT COMPARES THE NUMBER OF INVIVIUALS       | A 900  |
| C      | TUDIVIDUALS IN A PRESED MINIMUM, IN THE NUMBER OF          | A 507  |
| C      | NOT PROBABILISTIC IN THE FINAL STEPS AUT THE SPECIES HAS   | A 589  |
| Č      | VARIED PROBABILISTICALLY. AND THIS CONTROLS THE NUMBER     | A 5/8  |
| C      | OF INDIVIDUALS.  | A 5/1  |
| C      |  | A 5/2  |
|        | IF (111ND(L1)-HINNO) 78,78,71                              | A 5/3  |
| 73     | PRINT 116, L1, AGE(L1)                                     | A 5/4  |
|        | NEXTC=NEXTC+1  | A 5/5  |
| 74     |  |        |
| 1      | CHALLENCE DE NEWTO   |        |
| C      | LUTAL TTV TUTACTIC   | A 5/9  |
| č      | FOLLOWING IS THE SPECIATION PART OF THE MODEL.             | A 500  |
| C      | NAREA HEGATIVE INDICATES NEW AREA IS AVAILABLE FOR SPECIES | A 501  |
| C      | COLONIZATION, OR THAT RESOURCES ARE INCREASING.            | A 502  |
| С      |  | A 583  |
|        | IF (NAREA) 72,73,73  | A 584  |
| ~ 12   | AREASAREA+DAREA  | A 202  |
| C<br>C | VIRGAT DECIFATE THE SPERICE RENGITY.                       | A 587  |
| C      | STUSKT REFELLIS THE SPECIES DENSITY.                       | A 588  |
| 75     | NICSAT&NSPECP/ARFA   | 589    |
|        | KOUNTES  | A SYE  |
|        | D0 82 1=1, HSPEC   | A 5Ý1  |
|        | IF (11KD(1).LE.20) GO TO 82                                | ¥ 245  |
|        | RJ=RANF(-1)  | A 593  |
| ~      | IF (NICSAI+R3) 74,82,82                                    | A 274  |
|        | PISON IS THE FINAL TUREGUOIN FOR SPECIATION _ OPERIES WITH | A 595  |
| Č      | HIGHER RELATIVE VARIABILITY ARE GIVEN HIGHER               | A 597  |
| C      | PROBABILITIES FOR SPECIATION.                              | A 598  |
| C      |  | A 599  |
| 74     | PISOL=AVEVAR(I)/HAXVAR                                     | N 640  |
|        |  |        |

|     | PRUGRAM MEPRO (INFUL;OUTPUT;TAPEOW4IMPUT;TAPEO1=OUTPU;)        |         |
|-----|--|---------|
|     | R4=RANF(-1)  | A 601   |
|     | IF (R4_PISOL) 75.82.82   | A 602   |
| 75  |  | - A 693 |
|     | HENSPEC+KOUNT  | A 604   |
|     | R5=RANF(-1)  | A 605   |
|     | RÓBRANF (-1)   | A 606   |
|     | R7=RANF(-1)  | A 607   |
| С   |  | A 698   |
| C   | NEW SPECIES CENTER IS LOCATED.                                 | A 609   |
| C   |  | A 618   |
|     | X(H)=X(1)+R5+(2+CLDIST)  | A 611   |
|     | Y(M)=Y(I)+R6+(2+CLDIST)  | A 612   |
|     | 2(H)=2(])+R7+(2+CLDIST)  | V 013   |
|     | AGE(M)=0.  | - A 614 |
|     | CANOI(M)=75.   | A 615   |
|     | PRINT 118, I,M   | A 616   |
| C   |  | A 617   |
| C   | NEW SPECIES ARE GIVEN A NUMBER OF INDIVIDUALS EQUAL TO         | A 618   |
| C   | 40 PERCENT OF THE NUMBER IN PARENT SPECIES.                    | A 619   |
| С   |  | A 628   |
|     | NIND(M) = , 40 = NIND(I)                                       | A 621   |
| -   | J≢Ø  | A 622   |
| C   |  | A 023   |
| C   | COURDINATES OF CLASSES IN NEW SPECIES ARE ASSIGNED.            | A OZA   |
| C   |  | A 623   |
|     |  | A DCO   |
|     |  | A 02/   |
|     |  | A 020   |
|     | JEUTA<br>8007 / M. I / Y. M                                    | A DET   |
|     |  | A 0.00  |
|     |  | A 0.31  |
| 74  | CONCERTS SECTORED ALL AND CONTENTS                             |         |
| 73  |  | A 0.34  |
| 78  |  | A 635   |
|     |  | A 6.56  |
| C   |  | A 637   |
| Č   | ASSIGNMENT OF OPEN AND CLOSED CLASSES FOR NEW SPECIES FOLLOWS. | A 638   |
| C   |  | A 639   |
| •   | READ 119, (SPECIE(H,J).J=1.27)                                 | A 640   |
|     | PACKSPACE 60   | A 641   |
|     | BACKSPACE 60   | A 642   |
|     | J=0  | A 643   |
|     | 11D=11ND(H)  | A 644   |
|     | D0 61 N#1,NID  | A 645   |
| 73  |  | A 646   |
|     | IF (J,GT,27) J=1   | A 647   |
|     | 1F (SPECIE(H, J)) 79,80,80                                     | A 648   |
| 8 4 | SPECIE(M, J) =SPECIE(M, J) +1                                  | A 649   |
| 81  | CONTINUE   | A 65    |
|     |  |         |

PROGRAM REPRO (INPUT.OUTPUT.TAPE684INPUT.TAPE61=OUTPUT)

```
PROGRAM REPRO (INPUT, OUTPUT, TAPE60=INPUT, TAPE61=OUTPUI)
   82
          CONTINUE
                                                                               A 671
        PRINT 128, IM, KOUNT
                                                                               A 652
C
                                                                               A 653
        LSPEC IS INCREMENTED AS NEW SPECIES ARE ADDED.
                                                                               A 624
C...,
C
                                                                               A 655
        IF (KOUNT, GT, Ø) NSPEC=H
                                                                               A 656
                                                                               A 657
        COUNTES
        00 85 1=1, NSPEC
                                                                               A 658
          IF (410(1)) 64,84,83
CONTINUE
                                                                               A 659
   83
                                                                               A 668
          AGE(1)=AGE(1)+1
                                                                               A 601
                                                                               A 602
          GO TO 85
   84
          COUNT=COUNT+1
                                                                               A 663
       .
   87
          CONTINUE
                                                                               A 664
С
                                                                               A 665
        NUMBER OF EXTINCT SPECIES ARE TABULATED AND SUBTRACTED FROM
C...
                                                                               A 666
        NSPEC TO GIVE NSPECP -- THE NUMBER OF SPECIES PRESENT,
C...,
                                                                               A 601
                                                                               A 668
C
        I.SPECP=NSPEC-COUNT
                                                                               A 669
                                                                               A 6/8
   86
        CONTINUE
                                                                               A 6/1
С
C .... THE FOLLOWING STATEMENTS TABULATE THE NUMBER OF EXTINCT AND
                                                                               A 6/2
C..., EXTANT SPECIES, AND THEIR DURATIONS SO THAT SURVIVORSHIP
                                                                               A 6/3
C ... CURVES CAN BE DRAWN.
                                                                                 6/4
                                                                               A
C
                                                                               A 6/5
      PRINT 121
                                                                               A 6/6
      DO 89 1=1,NSPEC
                                                                                 617
                                                                               ٨
                                                                               A 6/8
        1F (NIND(1)) 87,87,88
   87
        PRINT 116, I,AGE(I)
                                                                               A 6/9
                                                                               A 086
        GO TO 99
   88
        PRINT 122, I,AGE(I)
                                                                               A 681
                                                                               A 682
   89
        CONTINUE
                                                                               A 683
      PRINT 123
      NGENBHGEN+1
                                                                               A 684
      00 93 J=1, NGEN
                                                                               A 685
                                                                               A 686
   90
        CIN(J)=0.0
      EXTSPEC=7.0
                                                                                 687
                                                                                A
                                                                               A 608
      PIGAGE=0.0
      DO 92 1=1,NSFEC
                                                                               A 689
                                                                               A 690
        IF (NIND(1),EQ.0) GO TO 91
        CO TO 92
                                                                               A 691
   91
        FXTSPEC=FXTSPEC+1
                                                                                 692
                                                                               A
        IF (AGE(1), GT, BIGAGE) BIGAGE=AGE(1)
                                                                               A 693
                                                                                 6Ÿ4
        J=AGE(1)
                                                                               ٨
                                                                                 6ÿ5
        CTN(J)=CTN(J)+1
                                                                               ٨
                                                                               A 696
   92
        CONTINUE
                                                                               A 697
      CUHFRQ=0.2
                                                                               A 698
      DO 93 J=1,BIGAGE
                                                                               A 699
        CUMFRQ=CUMFRG+CTN(J)
                                                                                A 708
        SPECR = EXTSPEC-CUMFRQ
```

|   |       | PRINT 124, J,SPECR,J,CTN(J)  | A        | 7Ø1   |
|---|-------|--|----------|-------|
|   | 93    | CONTINUE   | A        | 105   |
|   |       | PRINT 125  |          | 705   |
|   |       | D0 94 J#1.NGEN   |          | 104   |
|   | 04    |  | 7        | 205   |
|   |       |  | -        | 7     |
|   |       |  | <b>.</b> | 100   |
|   |       | 00 95 1=1, NSPEC   | •        | 101   |
|   |       | IF (AGE(I),GT,BIGAGE) BIGAGE=AGE(I)  | A        | 169   |
|   |       | J=AGE(1)   | A        | 709   |
|   |       | CTN(J)=CTN(J)+1  | A        | 712   |
|   | 95    | COUTINE  | Ä        | /11   |
|   |       |  | Â        | 712   |
|   |       |  | -        | 198   |
|   |       |  | -        | 710   |
|   |       |  | A        | 117   |
|   |       | SPECREIISPEC-CUMFRO  |          | /17   |
|   |       | PRINT 124, J.SPECR.J.CTN(J)  | A        | /16   |
|   | 96    | CONTINUE   |          | 717   |
|   |       | PRINT 126  | A        | /10   |
|   |       | DO 97 JEL-NGEN   |          | 719   |
|   | 97    |  |          | 120   |
|   |       |  | 7        | 121   |
|   |       | $\begin{array}{c} \mathbf{D} \in \{0, 1, 0\} \\ \mathbf{D} \in \{0, 0\} \\ \mathbf{D} \in \{\mathbf$ | 2        | 122   |
|   |       |  | •        | 166   |
|   |       | 16 (MIAD(1) - 01 - 00 - 10 - 08  |          | 123   |
|   |       | GU TU 99   | •        | 124   |
|   | 98    | IF (AGE(I),GT,BIGAGE) BIGAGE=AGE(I)  |          | 152   |
|   |       | J=AGE(1)   | A        | 150   |
|   |       | CTN(J)=CTN(J)+1  | A        | 727   |
|   | 99    | CONTINUE   |          | 128   |
|   |       | CUMFR0=0.0   |          | 729   |
|   |       | DO 133 JE1.BIGAGE  |          | 738   |
|   |       |  | Ĩ        | 7.51  |
|   |       |  | 2        | 132   |
|   |       |  |          | 1.1.  |
|   | 4.0.4 |  |          | 7 4 4 |
| _ | 100   | CONTINUE   |          |       |
| С |       |  |          | 137   |
|   | 121   | FORMAT (15,12,3F0,3,12)  | •        | 130   |
|   | 165   | FORMAT (7F6,1)   | A        | 757   |
|   | 103   | FO9MAT (7X,17,5F7.2)   | A        | 138   |
|   | 134   | FOPMAT (3F7.2)   | A        | 759   |
|   | 125   | FORMAT (13.2F6.1)  | A        | 148   |
|   | 126   | FORMAT (1665, 2/1165 0)  |          | 741   |
|   | 127   | Enguat (4012/4012/4012/4012/212)   | Â        | 142   |
|   | 404   |  | Ā        | 143   |
|   | 100   | FORMAT (AUL ISTUIR IS THE BECTANNING OF CENEDATION IE)   | ~        | 744   |
|   | 107   | FORMAT (10- AUEVAL ET A AUEVAL ET A AU CALL ET A)  | <u>,</u> | 224   |
|   | 119   | PUNHAI LING, THEALS, PICESANDELS, PICESANDELS ESTERPICE  | Ă.       | 141   |
|   | 111   | POHMAT (1H-, MSPECIES, P. 2, 45H IS IN PAVORED POSITION AND HAS CANO   |          | 190   |
|   | :     | 1N VALUE =,F7,2)   |          | 141   |
|   | 112   | FORMAT (1H0,12H GENERATION,14,45H AVERAGE SURVIVAL RATE FOR ALL  | A        | 140   |
|   | :     | 1 SPECIES =,F7,2)  |          | 149   |
|   | 113   | FORMAT (1H0,10x,31HTHE NUMBER OF SPECIES PRESENT =,14)   | A        | 128   |

| 114 FORMAT (140,10x,42HTHE NUMBER OF INDIVIDUALS IN SPECIE SPACE   | .0 A 751       |
|--|----------------|
| 1)<br>115 CORMAT (14. 364THE NUMBER OF INDIVIDUALS IN SPECIES 14 3-4 AFTER   | A /22<br>A /53 |
| 1 SETERATION AND REPORT OF INDITIONES IN SECTOR $3,3,9,9,9,9,9,9,9,9,9,9,9,9,9,9,9,9,9,9$  | A 754          |
| 16 FORMAT ALLO 194 AND REPRODUCIONESISSEN SURVIVAL PERCENT -1'''E  |                |
| TTO FURTHAL (THATTOAT/HSPECIES/14/34 13/F/16/200 UNITS ULD AND 10 EAT  |                |
| 1077 COMMENTED AND ANTATAL MUMORS OF SYTING SPECIES SUBIME SEMERAL   | A /30          |
| 11. TO TAL (140, 14, 90 IOTAL NUMBER OF EATING SPECIES DURING GENERA   |                |
| 1041 TODAT SHE ANY ACCOMPANY ADVANCE IN A ANY ACCOUNTED ADVANTED | A /20          |
| 110 FUMMAI (140,104,104PARENI SPECIES #,14,204 DAUGHIER SPECIES #,1  | 4) A /29       |
| 117 FURNAL (10F5:0/11F5.0/   | A /OF          |
| IZE FURNAL (ING, TEX, SANTHE NUMBER OF NEW SPECIES IN GENERALIUN, 14, IN   | A /01          |
| 115)   | ¥ 102          |
| 121 FORMAT (1H1, 32HRAW DATA FOR SURVIVORSHIP CURVES)  | A 703          |
| 122 FORMAT (1HØ,10%,7HSPECIES,14,3H IS,F7,2,24H UNITS OLD AND IS EXT   | AN A 704       |
| 17)  | A 705          |
| 123 FORMAT (1H1,10×,52HTHE FOLLOWING ANALYSIS INCLUDES ONLY EXTINCT S  | SP A 706       |
| 1ECIES)  | A 767          |
| 124 FORMAT (1H0,10X,9HOURATION:,14,20H SPECIES REMAINING:,F5.0,27H   | N A 768        |
| 1UMRER OF SPECIES LASTING, 14, 13H GENERATIONS=, F7.8)   | A 709          |
| 129 FORMAT (1H-, 43HTHE FOLLOWING ANALYSIS INCLUDES ALL SPECIES)   | A 778          |
| 126 FORMAT (1H1, 51HTHE FOLLOWING ANALYSIS INCLUDES ONLY LIVING SPECI  | ES A //1       |
| 1)   | A //2          |
| END  | A 773-         |

```
C
                                                                                                                   1
2
                                                                                                              8
C..., SUPPROGRAM NORMAL IS USED TO CNOOSE PARAMETERS FROM A
C..., NORMAL DISTRIBUTION WHICH HAS SPECIFIED MEAN AND
C..., STANDARD DEVIATION,
                                                                                                              8
                                                                                                              8
                                                                                                                    3
                                                                                                                    Ă
                                                                                                              B
C
                                                                                                              B
                                                                                                                    5
         SUBROUTINE NORMAL (EX, STDX, X)
                                                                                                              B
                                                                                                                    6
         SUM=3,
DO 1 1=1,12
R8=RANF(-1)
SUM=SUM+R8
                                                                                                                   7
                                                                                                              8
                                                                                                              8
                                                                                                                    8
                                                                                                              ē
                                                                                                                   9
                                                                                                                  10
                                                                                                              0
B
          CONTINUE
      1
        X=STDX+(SUH-6,8)+EX
                                                                                                                  12
13
14-
                                                                                                             8
         RETURN
         END
                                                                                                              Ð
         SUBROUTINE SORT (N,X)
                                                                                                             C
                                                                                                                   1
        DIMENSION X(200)
INTEGER BOTOH, SWICH, I.N
REAL X, T
                                                                                                                   2
                                                                                                             00000000
                                                                                                                   3
                                                                                                                    4
                                                                                                                   5
C
C..., FORTRAN SUBPROGRAM FOR ORDERING SPECIES AND CLASSES FROM C.... FITNESS OPTIMUM,
                                                                                                                   7
                                                                                                                   8
C
                                                                                                             0000
                                                                                                                   9
        BOTOM=N-1
     1 SWICH=1
                                                                                                                  12
        00 3 1=1,80TOM
                                                                                                                  11
                                                                                                                  12
           1F (X(1)-X(1+1)) 3,3,2
                                                                                                             C
C
                                                                                                                  13
      2 T=X(1)
                                                                                                                  14.
           X(1)=X(1+1)
X(1+1)=T
                                                                                                             C
C
                                                                                                                  15
                                                                                                                  16
17
           SWICH#I
     S CONTINUE
IF (SWICH-1) 4,5,4
                                                                                                              C
C
C
C
                                                                                                                  18
                                                                                                                  19
28
      4 90TUM=SWICH-1
                                                                                                              Č
        GO TO 1
                                                                                                              C
                                                                                                                  21
      5 RETURN
                                                                                                                  22-
        END
                                                                                                              C
```

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## LIST OF REFERENCES

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